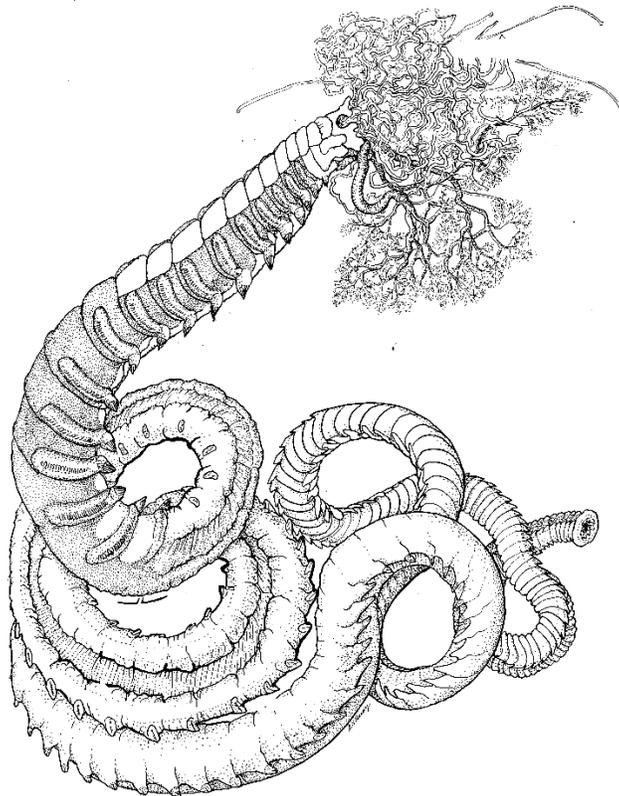


Oregon Estuarine Invertebrates: Rudys' Illustrated Guide to Common Species



3rd edition, 2016

Edited by Terra C. Hiebert, Barb Butler and Alan Shanks

Original edition by Paul and Lynn Rudy

Please email corrections to oimb@uoregon.edu

A publication of the
University of Oregon Libraries
and the
Oregon Institute of Marine Biology
2016

Introduction:

Lynn and Paul Rudy first published Oregon Estuarine Invertebrates: An Illustrated Guide to the Common and Important Invertebrate Animals (OEI) in 1983. It contained 110 descriptions with a single page of text facing Lynn's amazing illustration of each species. As they stated in their introduction, this work was intended to be updated as new information became available. It was not intended to be a key but rather a guide for students and researchers in Oregon, Washington and northern California. They created a 30-species supplement in the early 1980s, but it was unfortunately lost for a time by their USFWS publishing partner. It turned up years later upon his retirement and subsequent office cleaning.

In retirement, Lynn and Paul gave permission to OIMB staff to continue updating their publication. In 2005, the 1983 edition of OEI was digitized and made freely available in University of Oregon's institutional repository (Scholars' Bank): <http://hdl.handle.net/1794/1070>. Several years later the missing species descriptions were returned to OIMB and incorporated into the existing, and digitized work. Two OIMB graduate students digitized each of the 140 illustrations and replaced the Leroy Lettering Set labels with computer generated text. The bibliographies were also fleshed out, giving full citations for each work and pointing to individual chapters within cited monographs. We also included updated taxonomic names where necessary and published this in Scholars' Bank as the Second Edition of OEI: <http://hdl.handle.net/1794/12938>. To facilitate future updates, each species description was also published as a separate chapter, each containing footnotes directing readers to send suggested corrections or updates to OIMB staff.

While the Second Edition of OEI contained additional species descriptions, fuller bibliographies and re-labelled illustrations, there was no additional content aside from relabeling with current taxonomic names. As part of a Winter 2014 Graduate Seminar, OIMB students updated 18 of the chapters. Two students authored new species descriptions and one was able to split a basic description of *Littorina* sp. into individual descriptions for *Littorina plena* and *Littorina scutulata*. At this point, OEI truly became a collaboration among OIMB students and faculty. The greatest step forward occurred in Fall 2014 when the University of Oregon Libraries provided funding for Terra C. Hiebert to incorporate new information from the intervening 30 years in this now open-access publication. Clara D. Piazzola helped with the eight cnidarian species and Barb Butler and Alan Shanks served as editors for the entire volume. Over this 1.5-year period, Terra standardized the edits made by her fellow students; revised 126 of the (now) 142 descriptions; and when necessary added a "taxonomy" section at the beginning of the description to clarify changes that have occurred through the years. These species descriptions are available as individual chapters within Scholars' Bank and in 2016 the full Third Edition was published under the updated subtitle of Oregon Estuarine Invertebrates: Rudys' Illustrated Guide to Common Species (<http://hdl.handle.net/1794/18839>). Future OIMB Invertebrate Zoology students will update the remaining species descriptions, continuing the collaborative tradition started by the Rudys.

We have added an index to common names, as well as names previously used in this guide, and include a map of the Coos Bay area to help students locate sampling sites mentioned in the text. An online index points to all of the species descriptions in Scholars' Bank: <http://researchguides.uoregon.edu/oei>. We consider the publication date for the entire volume to be 2016, but have noted when an individual species description was updated in 2014 or 2015. Species are grouped by phyla, then grouped by order or class, then alphabetically by

family and finally alphabetically by genus. We also include an overall A-Z list by species name for those not familiar with invertebrate nomenclature.

A number of students have assisted with this publication. Many thanks to Megan Grupe (nee Copley) and Sara Okum (nee Williams) for their work on the illustration labels and to Heidi Harris and Jennifer Schmitt for their work on the bibliography and text formatting. Unless denoted by the presence of a co-author, all species descriptions are by Terra C. Hiebert. Unless otherwise noted, all illustrations are the work of Lynn Rudy. While the content has been updated, we have kept the tried-and-true format that Lynn and Paul established for OEI, in particular the “Possible Misidentification” section that is so useful to students. As you scan the bibliographies you will note our reliance on a number of important works, including The Light and Smith Manual, and James T. Carlton was our primary source for any taxonomic questions.

A number of OIMB alumni have contributed funds to underwrite the cost of future updates to OEI as well as covering the cost of Rite-in-the-Rain paper and large-format binders to make multiple copies of OEI available in all OIMB teaching laboratories.

Suggested citation format for OEI chapters:

Hiebert, T.C. and L. Rasmusson. 2016. *Cancer magister*. In: *Oregon Estuarine Invertebrates: Rudys' Illustrated Guide to Common Species*, 3rd ed. T.C. Hiebert, B.A. Butler and A.L. Shanks (eds.). University of Oregon Libraries and Oregon Institute of Marine Biology, Charleston, OR.

We dedicate this work to the Rudys for all they have done for OIMB and its students.

Phylum	Class/Order	Family	Genus and species	Page
--------	-------------	--------	-------------------	------

Cnidaria (*Sea anemones and allies*)

Hydrodia	Aequoreidae	<i>Aequorea victoria</i>	2
	Campanularidae	<i>Obelia longissimi</i>	8
	Corynidae	<i>Polyorchis penicillatus</i>	14
	Tubulariidae	<i>Ectopleura crocea</i>	20
Actiniaria	Actiniidae	<i>Anthopleura artemisia</i>	26
		<i>Anthopleura elegantissima</i> ...	32
	Diadumenidae	<i>Diadumene lineata</i>	38
	Edwardsiidae	<i>Nematostella vectensis</i>	44
	Metridiidae	<i>Metridium senile</i>	50

Nemertea (*Ribbon worms*)

Palaeonemertea	Carinomidae	<i>Carinoma mutabilis</i>	56
	Tubulanidae	<i>Tubulanus polymorphus</i>	60
		<i>Tubulanus sexlineatus</i>	64
Heteronemertea	Lineidae	<i>Cerebratulus californiensis</i>	68
		<i>Cerebratulus marginatus</i>	72
		<i>Ramphogordius sanguineus</i> ..	76
Hoplonemertea	Amphiporidae	<i>Amphiporus imparispinosus</i> ...	80
	Emplectomenatidae	<i>Paranemertes peregrina</i>	84

Annelida (*Segmented worms*)

Capitellida	Arenicolidae	<i>Abarenicola pacifica</i>	90	
	Capitellidae	<i>Capitella</i> spp.....	94	
Opheliida	Opheliidae	<i>Mediomastis californiensis</i> ...	100	
		<i>Armandia brevis</i>	104	
		<i>Ophelia assimilis</i>	108	
		<i>Thoracophelia mucronata</i>	112	
Orbiniida	Orbiniidae	<i>Leitoscoloplos pugettensis</i> ...	116	
	Paraonidae	<i>Paraonaella platybranchia</i>	122	
Oweniida	Oweniidae	<i>Owenia collaris</i>	126	
Phyllodocida	Glyceridae	<i>Glycera robusta</i>	132	
	Goniadidae	<i>Glycinde armigera</i>	138	
	Lumbrineridae	<i>Scoletoma zonata</i>	142	
		<i>Nephtys caeca</i>	146	
	Nephtyidae	<i>Nephtys caecoides</i>	152	
		Nereididae	<i>Neanthes brandti</i>	158
		<i>Neanthes limnicola</i>	164	
		<i>Nereis vexillosa</i>	170	
	Phyllodocidae		<i>Eteone lighti</i>	176
			<i>Eteone pacifica</i>	182

Phylum	Class/Order	Family	Genus and species	Page
--------	-------------	--------	-------------------	------

Annelida continued

		Polynoidae	<i>Halosydna brevisetosa</i>	188
			<i>Hesperonoe complanata</i>	192
	Sabellida	Sabellidae	<i>Eudistylia vancouveri</i>	196
	Spionida	Magelonidae	<i>Magelona sacculata</i>	202
		Spionidae	<i>Boccardia proboscidea</i>	208
			<i>Polydora nuchalis</i>	214
			<i>Pseudopolydora kemp</i>	218
			<i>Pygospio elegans</i>	224
			<i>Scolelepis foliosa</i>	230
	Terebellida	Ampharetidae	<i>Hobsonia florida</i>	236
		Terebellidae	<i>Pista pacifica</i>	242
			<i>Thelepus crispus</i>	246

Sipuncula (Peanut worms)

	Phascolosomaformes	Phascolosomatidae	<i>Phascolosoma agassizi</i>	252
--	--------------------	-------------------	------------------------------------	-----

Arthropoda (Crustacea)

Amphipoda	Gammaridea	Ampithoidae	<i>Ampithoe lacertosa</i>	258	
			<i>Ampithoe valida</i>	264	
			<i>Eogammarus confervicolus</i> ..	270	
			<i>Grandidierella japonica</i>	276	
			<i>Americorophium brevis</i>	282	
			<i>Americorophium salmonis</i> ...	288	
			<i>Americorophium spinicorne</i>	294	
			<i>Eohaustorius estuarius</i>	300	
			<i>Allorchestes angusta</i>	306	
			<i>Eobrolgus spinosus</i>	310	
			<i>Megalorchestia pugettensis</i>	316	
			<i>Traskorchestia traskiana</i>	322	
			<i>Caprella drepanochir</i>	328	
			<i>Neotrypaea californiensis</i> ...	336	
Decapoda	Caprellidea	Caprellidae	<i>Caprella drepanochir</i>	328	
		Anomura	Callianassidae	<i>Neotrypaea californiensis</i> ...	336
			Paguridae	<i>Pagurus hirsutiusculus</i>	366
			Porcellanidae	<i>Petrolisthes cinctipes</i>	352
			Upogebiidae	<i>Upogebia pugettensis</i>	358
	Brachyura		Cancridae	<i>Cancer antennarius</i>	366
		<i>Cancer magister</i>		372	
		<i>Cancer oregonensis</i>		380	
		<i>Cancer productus</i>		386	
		<i>Pugettia producta</i>		392	
		Epiplatidae	<i>Pugettia producta</i>	392	
		Grapsidae	<i>Pachygrapsus crassipes</i>	398	
		Panopeidae	<i>Rhithropanopeus harrisi</i>	404	

Phylum	Class/Order	Family	Genus and species	Page
--------	-------------	--------	-------------------	------

Arthropoda continued

		Pinnotheridae	<i>Pinnixa faba</i>	410
			<i>Scleroplax granulata</i>	416
		Varunidae	<i>Hemigrapsus nudus</i>	422
			<i>Hemigrapsus oregonensis</i> ...	428
Caridea		Crangonidae	<i>Crangon alaskensis</i>	434
			<i>Crangon franciscorum</i>	440
			<i>Lissocrangon stylirostris</i>	446
		Thoridae	<i>Heptacarpus paludicola</i>	452
			<i>Heptacarpus sitchensis</i>	458
Cumacea		Lampropidae	<i>Lamprops quadriplicata</i>	464
		Leuconidae	<i>Nippoleucon hinumensis</i>	470
		Nannastacidae	<i>Cumella vulgaris</i>	476
Isopoda		Chaetiliidae	<i>Mesidotea entomon</i>	482
		Detonidae	<i>Detonella papillicornis</i>	490
		Idoteidae	<i>Idotea resecata</i>	504
			<i>Idotea wosnesenskii</i>	510
		Janiridae	<i>Ianiropsis derjugini</i>	512
		Ligiidae	<i>Ligia pallasii</i>	518
		Limnoriidae	<i>Limnoria tripunctata</i>	526
		Sphaeromatidae	<i>Gnorimosphaeroma insulare</i>	532
Mysidacea		Mysidae	<i>Archaeomysis grebnitzkii</i>	538
			<i>Neomysis mercedis</i>	546
Tanaidacea		Leptocheliidae	<i>Leptochelia</i> spp.....	554
Thoracica		Archaeobalanidae	<i>Semibalanus cariosus</i>	560
		Balanidae	<i>Balanus crenatus</i>	568
			<i>Balanus glandula</i>	574
			<i>Balanus nubilus</i>	586

Mollusca (*Mussels, clams, snails and slugs*)

Gastropoda	Archeogastropoda	Lottidae	<i>Lottia digitalis</i>	588
			<i>Lottia pelta</i>	592
		Trochidae	<i>Chlorostoma funebris</i>	596
Caenogastropoda		Hydrobiidae	<i>Lithoglyphus virens</i>	600
Mesogastropoda		Assimineidae	<i>Assiminea californica</i>	604
		Lacunidae	<i>Lacuna porrecta</i>	608
		Littorinidae	<i>Littorina plena</i>	612
			<i>Littorina scutulata</i>	618
			<i>Littorina sitkana</i>	624
		Pleuroceriadae	<i>Juga plicifera</i>	628
Neogastropoda		Olividae	<i>Callianax biplicata</i>	632
		Thaisidae	<i>Nucella lamellose</i>	636
			<i>Nucella ostrina</i>	640
Nudibranchia		Facelinidae	<i>Hermisenda crassicornis</i> ...	644
		Onchidoidae	<i>Onchidoris bilamellata</i>	650
Pulmonata		Ellobiidae	<i>Myosotella myosotis</i>	654
Sacoglossa		Hermaeidae	<i>Alderia modesta</i>	658
			<i>Aplysiopsis enteromorphae</i>	662

Phylum	Class/Order	Family	Genus and species	Page
--------	-------------	--------	-------------------	------

Mollusca continued

Bivalvia	Myoida	Hiatellidae	<i>Hiatella arctica</i>	666	
		Myidae	<i>Cryptomya californica</i>	674	
			<i>Mya arenaria</i>	680	
		Pholadidae	<i>Penitella penita</i>	690	
			<i>Zirfaea pilsbryi</i>	698	
			<i>Bankia setacea</i>	706	
		Mytiloidea	Teredinidae	<i>Adula californiensis</i>	714
			Mytilidae	<i>Mytilus trossulus</i>	720
		Pholadomyoidea	Lyonsiidae	<i>Entodesma navicula</i>	732
	Veneroidea		Cardiidae	<i>Clinocardium nuttallii</i>	738
		Corbiculidae	<i>Corbicula fluminea</i>	746	
		Mactridae	<i>Tresus capax</i>	756	
		Pharidae	<i>Siliqua patula</i>	764	
		Solenidae	<i>Solen sicarius</i>	772	
		Tellinidae	<i>Macoma balthica</i>	778	
			<i>Macoma inquinata</i>	788	
			<i>Macoma nasuta</i>	794	
			Veneridae	<i>Leukoma staminea</i>	802
			<i>Nutricola tantilla</i>	812	
		<i>Saxidomus giganteus</i>	820		

Phoronida (Horseshoe worms)

Phoronida	Phoronidae	<i>Phoronis pallida</i>	830
-----------	------------	-------------------------------	-----

Echinodermata (Sea stars and sea urchins)

Forcipulatida	Asteriidae	<i>Pisaster brevispinus</i>	836
		<i>Pisaster ochraceus</i>	842

Chordata (Tunicates)

Syolidobranchia	Styelidae	<i>Botrylloides violaceus</i>	850
-----------------	-----------	-------------------------------------	-----

Appendices

A: Alphabetical list of species by genus.....	855
B: Common and previous names used in this work.....	858
C: Local (Coos Bay) collection sites mentioned in this text	861

Cnidaria

Aequorea victoria

Crystal jelly

Phylum: Cnidaria
Class: Hydrozoa, Hydroidolina
Order: Leptomedusae
Family: Aequoreidae

Taxonomy: Originally described as *Mesonema victoria* (Murbach and Shearer, 1902), current synonyms and previous names for *Aequorea victoria* include *Aequorea aequorea*, *A. forskalea*, and *Campanulina membranosa* (a name proposed for the polyp form by Strong 1925) (Mills et al. 2007; Schuchert 2015). The taxonomy of Aequoreidae is currently in flux and awaiting further molecular research (Mills et al. 2007).

Description

General Morphology: *Aequorea victoria* has two forms. Its sexual morphology is a gelatinous hydromedusa. It has a wide bell, many tentacles, and radial canals that run from the mouth to the bell margin, where they are connected by a ring canal. Suspended from the inside of the bell by a peduncle is the manubrium, or mouth. A velum rings the inside of the bell margin (Fig. 1). Its asexual morphology is a small polyp. Each polyp has a stem (hydrocaulus), and most have a sheathed (thecate) hydranth with a mouth (manubrium), stomach, tentacles, and an operculum (Fig. 4). Rather than having hydranths, some polyps have gonophores (Fig. 5).

Medusa:

Size: *Aequorea victoria* is much wider than tall and can get up to 12 cm in diameter (Kozloff 1987), but only 4 cm in height (Arai and Brinckmann-Voss 1980).

Color: Adult specimens are transparent aqua blue with whitish radial canals, while juveniles have a green sub-umbrella, opalescent gray or milky gonads, and occasionally have brown tentacle bulbs (Arai and Brinckmann-Voss 1980). Mature specimens also fluoresce and luminesce, with their luminescence concentrated around the bell margin (Kozloff 1983).

Body:

Bell: The bell is large and relatively flat, and contracts when swimming. It is thick, gelatinous, and rigid, with a ring canal around the margin and radial canals running from the mouth to the margin (Fig. 1). It has a short, thick peduncle (Arai and Brinckmann-Voss 1980).

Radial Canals: *Aequorea victoria* individuals can have over 100 symmetrical, unbranched radial canals. In mature specimens all radial canals reach the bell margin (Mills et al. 2007, Kozloff 1987) (Figs. 1, 2). Excretory pores open at the canal bases near the tentacles (Hyman 1940).

Ring Canals: The ring canal surrounds the bell margin.

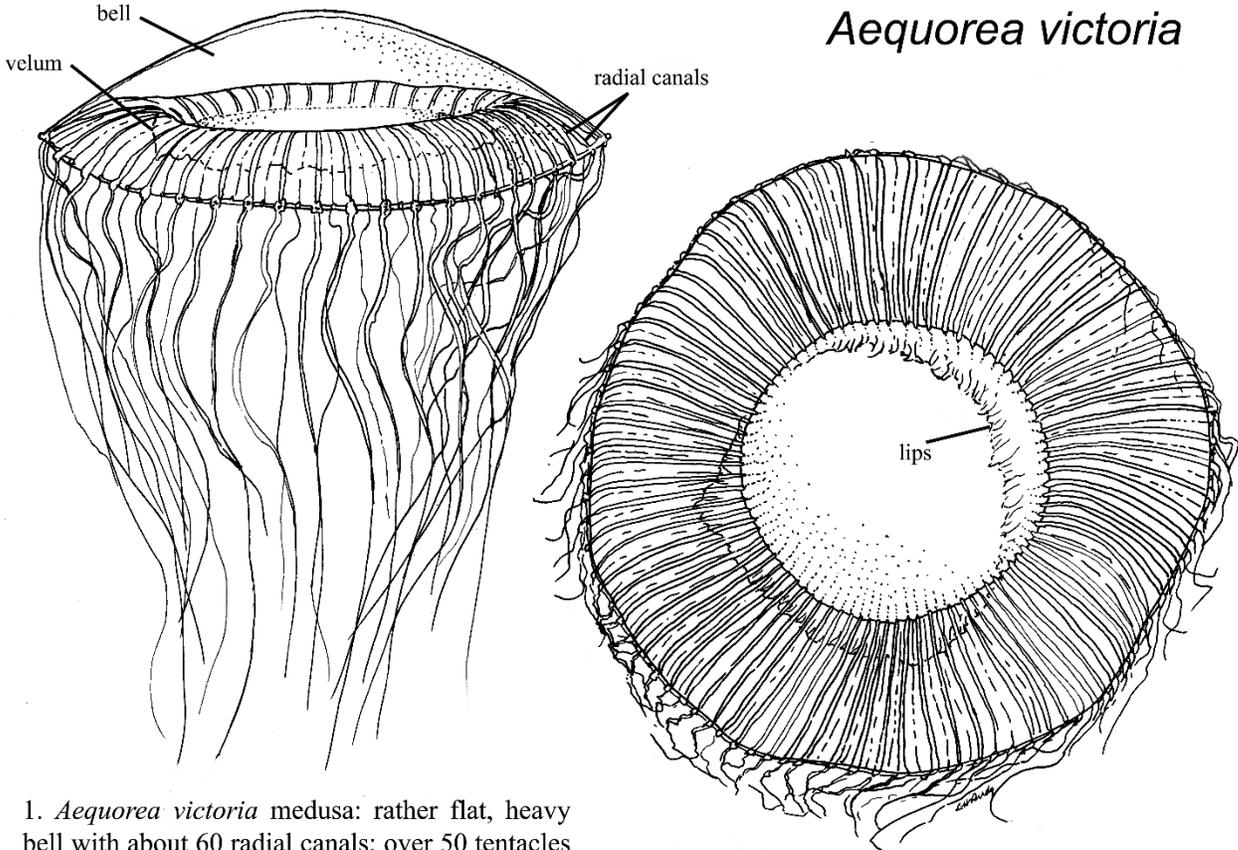
Mouth: The mouth is part of the tubular manubrium, which is large and surrounded by numerous frilled lips (Fig. 2).

Tentacles: The tentacles are hollow, unbranched, and numerous (up to 150, often about as many as radial canals) (Arai and Brinckmann-Voss 1980, Mills et al. 2007). They occur on a single whorl on the ring canal (Mills et al. 2007). Not all of the tentacles are the same length and they can be very long when extended (Kozloff 1987). They have stinging cells (nematocysts) used in prey capture and defense. According to Purcell (1989) these nematocysts are isorhiza and microbasic mastigophore, but there is variation in cnidoblast naming schemes between researchers.

Velum: The velum is a flap of tissue, barely visible inside the bell rim, which is used for swimming (Fig. 1) (Hyman 1940).

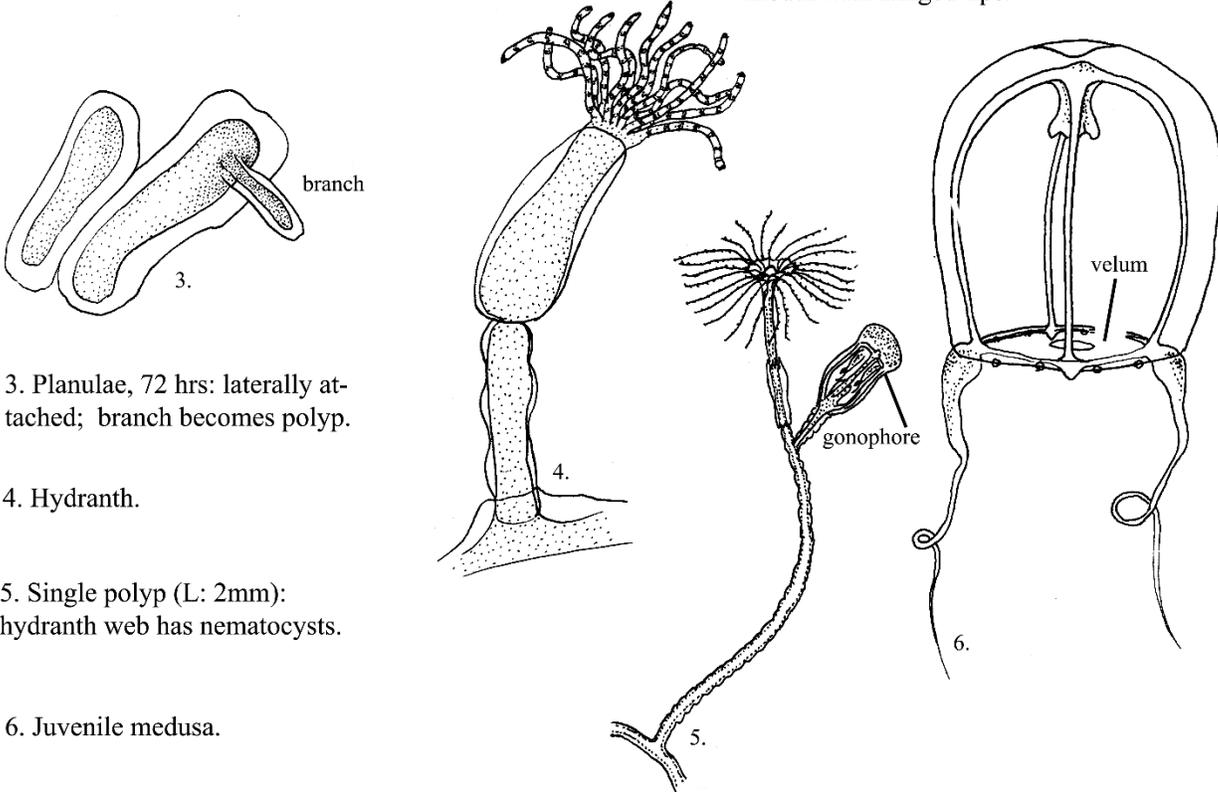
Gonads: Gonads in *A. victoria* are not finger-like as in many other hydromedusae. They develop once the bell diameter reaches 25 mm (Mills and Strathmann 1987), and are suspended from and span nearly the entire length of the radial canals (Fig. 1) (Mills et al. 2007, Kozloff 1987).

Aequorea victoria



1. *Aequorea victoria* medusa: rather flat, heavy bell with about 60 radial canals; over 50 tentacles on ring canal; wide mouth; gonads along radial canals.

2. Medusa: dorsal view; mouth with fringed lips.



3. Planulae, 72 hrs: laterally attached; branch becomes polyp.

4. Hydranth.

5. Single polyp (L: 2mm): hydranth web has nematocysts.

6. Juvenile medusa.

Sensory: *Aequorea victoria* lacks eyespots but has statocysts, which are used for balance and orientation in the water column (Kozloff 1983).

Polyp: Rare (Mills 2001).

Size: Very small (0.5-1 mm) (Figs. 3–5) and composed of simple or slightly branched colonies with rarely more than two polyps (Strong 1925).

Color:

Body:

Pedicel: The polyp is pedicellate (Kozloff 1987; Mills et al. 2007), with hydrocaulus (stem) up to 2.5 mm in length, and is ringed rather than spirally grooved (Mills et al. 2007).

Hydranth: Each polyp has about twenty tentacles, a mouth, and an intertentacular web armed with nematocysts. The colonies are stolonial (connected by horizontal shoots at the base of each hydrocaulus) (Mills et al. 2007). The hydranth is covered by a theca (hydrothecae) that is deeper than it is wide and is able to hold the entire hydranth when contracted (Mills et al. 2007; Kozloff 1987) and the hydrothecae are radially symmetrical and do not have true marginal cups (Mills et al. 2007). Instead, they have longitudinal striations with straight walls (Mills et al. 2007; Kozloff 1987), and the opercular valves are continuations of the hydrothecal margin (Mills et al. 2007; Kozloff 1987).

Gonangium: Some branches of a colony have gonophores (Fig. 5) that reproduce by releasing free, spherical medusae (Mills et al. 2007; Kozloff 1987).

Cnidae: The intertentacular web contains nematocysts (Mills et al. 2007).

Possible Misidentifications

The family Aequoreidae includes leptomedusae with numerous radial canals, gonads attached to the radial canals, a broad short stomach, but lacking marginal or lateral cirri (Arai and Brinckmann-Voss 1980). There is only one other *Aequorea* species locally: *A. coerulescens*. It is larger than *A. victoria* and having a bell that is up to 25 cm in width with three to six times as many tentacles as radial canals. It is also less common and lives

further offshore than *A. victoria* (Mills et al. 2007).

Aequorea victoria medusae are very large among hydrozoans, and this species is the only Leptomedusa with more than 24 radial canals (most have only four) (Rees and Hand 1975). The Scyphozoa, or true jellyfish, are large, have fringed mouth lobes, scalloped margins, no velum, and a complex pattern of radial canals (Rees and Hand 1975). Some scyphozoans also have prominent, pendant oral arms. Very young *A. victoria*, up to 4 mm in diameter, can look similar to *Polyorchis penicillatus* in shape (Fig. 6); additionally, the young *A. victoria* lack the many radial canals that they will develop as they mature, and so seem more similar to the *P. penicillatus* with its four radial canals (Russell 1953).

Ecological Information

Range: Type localities are Victoria Harbor, British Columbia and Puget Sound, Washington (Murbach and Shearer 1902). Found in temperate waters in both northern and southern hemispheres. Well known in Puget Sound and British Columbia.

Local Distribution: Oregon distribution includes most bays and nearshore waters.

Habitat: Medusae are found in plankton and harbors (e.g., Charleston boat basin). The attached, or polyp, forms have been found intertidally (Mills et al. 2007).

Salinity: Collected at salinities of 30 and cannot tolerate large fresh water influx (e.g., from storms, MacGinitie and MacGinitie 1949).

Temperature: A cold to temperate species.

Tidal Level: Medusae are pelagic, while polyps are intertidal.

Associates: The small anemone, *Peachia quinquecapitata*, is sometimes parasitic on *A. victoria* individuals (Puget Sound, Washington). *Aequorea victoria* ingests *P. quinquecapitata* larvae, and once inside the hydromedusae, the larvae feed on nutrients in the radial canals and gonads. These parasitic larvae grow and metamorphose into juveniles while still inside *A. victoria*. Ultimately, the juvenile leaves its host mid-water and may become ectoparasitic on another *A. victoria* host (Mills and Strathmann 1987).

The hydromedusae are also parasitized by larval and juvenile forms of *Hyperia medusarum*. *Aequorea victoria* provides a pelagic host on which hyperiid amphipods can overwinter (Boonstra et al. 2015, Towanda and Thuesen 2006).

Abundance: *Aequorea victoria* is one of the most common large medusae. At the right time of year, it can occur in great numbers locally. It was present in high densities in Puget Sound, Washington, from the early 1960s to the mid-1990s. At that time, thousands were collected by researchers for their aequorin (luminescent protein) and GFP (Green Fluorescent Protein). Since the mid-1990s, *A. victoria* populations have decreased in both number and size, though this trend may be due to environmental change as well as high takes (Friday Harbor) (Mills 2001).

Life-History Information

Reproduction: Hydrozoans provide a good example of alternation of generations. The sessile, polypoid colony is delicate and plant-like. Medusae develop asexually from buds on the colony and become free swimming. All medusae from a single colony are the same sex (diecious). Eggs are transparent and 100µm diameter (Mills and Strathmann 1987) and medusae spawn within several hours of daybreak or sundown (Mills and Strathmann 1987). Embryos become planula larvae, which settle and develop into new polypoids. The first hydranth forms about a week after settlement, and additional hydranths grow from unbranched stolons (Mills and Strathmann 1987).

Larva: Embryos become tiny planula larvae. Planulae are uniformly ciliated and usually oval or club-shaped. These larvae are non-feeding and free-swimming. They are armed with nematocytes, but lack an apical ciliary tuft and septa (see Fig. 3, Sadro 2001). These larvae settle on their sides (Fig. 3) and become new polyps (Figs. 4, 5) (Strong 1925). In culture, the larvae form within 24 hours of fertilization and settle within 3–12 days (Mills and Strathmann 1987).

Juvenile: Juveniles are free, spherical medusae. They have two tentacles and scattered exumbrellar nematocysts that form a broad ring on the lower half of the bell (Fig. 6) (Mills et al. 2007 and Kozloff 1987). They

are not considered mature until they reach about 50 mm in diameter (Mills and Strathmann 1987). Juvenile recruitment occurs in the spring (Larson 1986).

Longevity: Unknown.

Growth Rate: Medusae grow very quickly, especially as compared to anthozoans (MacGinitie and MacGinitie 1949). In laboratory conditions they grow from egg to polyp in less than six days (Strong 1925).

Food: Their diet consists predominately of soft-bodied prey (e.g. ctenophores, medusae, cannery refuse), but they also eat mature crustaceans, crustacean larvae (Purcell 1989), and polychaetes. They are an important predator of fish larvae and eggs (Purcell 1989), but once the fish larvae pass the post-yolksac stage they are better able to escape the medusae and are less commonly preyed upon (Purcell et al. 1987). They also participate in intraguild predation, eating other gelatinous species that compete for zooplankton (Purcell 1991). Their feeding response is mostly tactile (Hyman 1940) (i.e. they use their tentacles to capture prey, Purcell et al. 1987). Additionally, they can sense water-born chemicals produced by crustacean prey, *Artemia* (Arai 1991), though further research is required to fully understand this behavior.

Predators: *Aequorea victoria* is well protected by nematocysts (stinging cells). Giant sunfish (*Mola mola*) eat them, as do some nudibranchs and the hydromedusae *Stomatoca atra* (Arai and Jacobs 1980) and *Phacellophora camtschatica* (Towanda and Thuesen 2006).

Behavior: The small polypoid stage requires a well-sheltered place in order to attach. The floating medusa is the stage most commonly seen (Figs. 1, 2), but often exhibits high mortality after a storm or a sudden pulse of fresh water (MacGinitie and MacGinitie 1949). *Aequorea victoria* medusae are luminescent when stimulated, and provided the original source for the commonly-used green fluorescent protein (GFP) and the luminescent protein aequorin (Mills et al. 2007).

Bibliography

1. ARAI, M. N. 1991. Attraction of *Aurelia* and *Aequorea* to prey. *Hydrobiologia*. 216:363-366.
2. ARAI, M. N., and A. BRINCKMANN-VOSS. 1980. Hydromedusae of British Columbia and Puget Sound. *Canadian Bulletin of Fisheries and Aquatic Sciences*. 204:1-192.
3. ARAI, M. N., and J. R. JACOBS. 1980. Interspecific predation of common Strait of Georgia planktonic coelenterates: laboratory evidence. *Canadian Journal of Fisheries and Aquatic Sciences*. 37:120-123.
4. BOONSTRA, J. L., M. E. KONEVAL, J. D. CLARK, M. SCHICK, M. SMITH, and A. L. STARK. 2015. Milbemycin oxime (interceptor) treatment of amphipod parasites (Hyperiididae) from several host jellyfish species. *Journal of Zoo and Wildlife Medicine*. 46:158-160.
5. HYMAN, L. H. 1940. *The Invertebrates: Protozoa through Ctenophora*. McGraw-Hill, New York, London.
6. KOZLOFF, E. N. 1983. *Seashore life of the northern Pacific coast*. University of Washington Press, Seattle.
7. —. 1987. *Marine invertebrates of the Pacific Northwest*. University of Washington Press, Seattle.
8. LARSON, R. J. 1986. Seasonal changes in the standing stocks, growth rates, and production rates of gelatinous predators in Saanich Inlet, British Columbia. *Marine Ecology Progress Series*. 33:89-98.
9. MACGINITIE, G. E., and N. MACGINITIE. 1949. *Natural history of marine animals*. McGraw-Hill Book Co., New York.
10. MILLS, C. E. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia*. 451:55-68.
11. MILLS, C. E., A. C. MARQUES, A. E. MIGOTTO, D. R. CALDER, C. HAND, J. T. REES, S. H. D. HADDOCK, C. W. DUNN, and P. R. PUGH. 2007. Hydrozoa: polyps, hydromedusae, and siphonophora, p. 118-167. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley.
12. MILLS, C. E., and M. F. STRATHMAN. 1987. Phylum Cnidaria, Class Hydrozoa, p. 44-71. *In: Reproduction and development of marine invertebrates of the northern Pacific coast: data and methods for the study of eggs, embryos, and larvae*. M. F. Strathman (ed.). University of Washington Press, Seattle, WA.
13. MURBACH, L., and G. SHEARER. 1902. Preliminary report on a collection of medusae from the coast of British Columbia and Alaska. *Annals of Natural History*. 7:pp. 71-73.
14. PURCELL, J. E. 1989. Predation on fish larvae and eggs by the hydromedusa *Aequorea victoria* at a herring spawning ground in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*. 46:1415-1427.
15. —. 1991. Predation by *Aequorea victoria* on other species of potentially competing pelagic hydrozoans. *Marine Ecology Progress Series*. 72:255-260.
16. PURCELL, J. E., T. D. SIFERD, and J. B. MARLIAVE. 1987. Vulnerability of larval herring (*Clupea harengus pallasii*) to capture by the jellyfish *Aequorea victoria*. *Marine Biology*. 94:157-162.
17. REES, J. T., and C. H. HAND. 1975. Class Hydrozoa, p. 65-84. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
18. RUSSELL, F. S. 1953. *The Medusae of the British Isles*. University Press, Cambridge.
19. SADRO, S. 2001. Cnidaria (Coelenterata), p. 13-23. *In: An identification guide to the larval marine invertebrates of the Pacific Northwest*. A. L. Shanks (ed.). Oregon State University, Corvallis.

20. SCHUCHERT, P. 2015. *Aequorea victoria* (Murbach & Shearer, 1902), World Register of Marine Species: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=283998>. [Accessed 7/24/2015].
21. STRONG, L. H. 1925. Development of certain Puget Sound hydroids and medusae. III:383-399.
22. TOWANDA, T., and E. V. THUESEN. 2006. Ectosymbiotic behavior of *Cancer gracilis* and its trophic relationships with its host *Phacellophora camtschatica* and the parasitoid *Hyperia medusarum*. Marine Ecology Progress Series. 315:221-236.

Updated 2015

C.D. Piazzola and T.C. Hiebert

Obelia longissima

A floating dock hydroid

Phylum: Cnidaria
Class: Hydrozoa, Hydroidolina
Order: Leptothecata
Family: Campanularidae

Taxonomy: *Obelia longissima* was first described by Pallas in 1766. Synonymous include *Campanularia flabellata*, *Gonothyrea longissima*, *Laomeda flabellata*, *L. longissima*, *O. flabellata*, *Sertularia longissima* (WoRMS 2015). *O. lucifera* may also be a synonym (especially of the medusa form), but further research is necessary to be sure. There has been much debate over the species identities within the genus *Obelia* (Cornelius 1975; Arai and Brinckmann-Voss 1980). The taxonomy above was taken from the World Register of Marine Species (WoRMS 2015). In addition to confusion in the lower taxonomy, the higher taxonomy has undergone revision. The order Hydroida was determined to be synonymous with subclass Hydroidolina in 2004 (Schuchert 2015).

Description

General Morphology: *Obelia longissima* has two forms. The sexual form is a gelatinous hydromedusa. It has radial canals that run from the top of the peduncle to the bell margin, where they are connected by a ring canal. Suspended from the inside of the bell by a peduncle is the manubrium, or mouth. A velum rings the inside of the bell margin (Fig. 3). Its asexual morphology is a large polyp. Each polyp has a stem (hydrocaulus), and most have a sheathed (thecate) hydranth with a mouth (manubrium), stomach, and tentacles. Rather than having hydranths, some polyps have gonothecae (Fig. 2).

Medusa:

Size: Newly-released medusae are about 0.5 mm in diameter; as they mature, they grow to 5 mm in diameter (Cornelius 1975; Kozloff 1983).

Color: Medusae are primarily clear. Their tentacle bases, mouths, gonads, and stomachs are sometimes yellow to brown, while their gonads and mouths can be bright green (Puget Sound) (Arai and Brinckmann-Voss 1980).

Body:

Bell: The bell is very thin and flat, with a small stomach, no peduncle, and a rudimentary velum (Fig. 3). It is eversible (Arai and Brinckmann-Voss 1980).

Radial Canals: There are four straight radial canals, each containing a globular gonad (Fig. 3).

Ring Canal: The ring canal is narrow, with eight statocysts (balance structures) (Arai and Brinckmann-Voss 1980) and no ocelli (Fig. 3).

Mouth: The mouth has 4 small, simple lips (Arai and Brinckmann-Voss 1980); in mature specimens these contain nematocysts (Boero et al. 2007).

Tentacles: Tentacles are numerous, solid (as opposed to hollow), and short. There are usually 16-26 in young medusae (Ricketts et al. 1985; Mills and Strathmann 1987), and more develop as they mature.

Velum: Reduced (Arai and Brinckmann-Voss 1980)

Gonads: There are 4 round gonads on the middle of each radial canal (Arai and Brinckmann-Voss 1980).

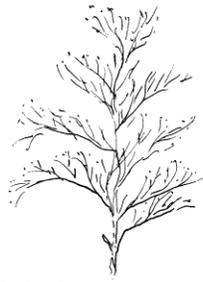
Polyp:

Size: Each colony can be up to 60 cm long (Mills et al. 2007) (Fig. 1). Older side branches are all about the same length (towards the base), but younger branches gradually get shorter near the growing tip (Mills et al. 2007).

Color: The polyp is transparent white when young, while old, mature colonies look dirty. Stems are brown to black (Mills et al. 2007).

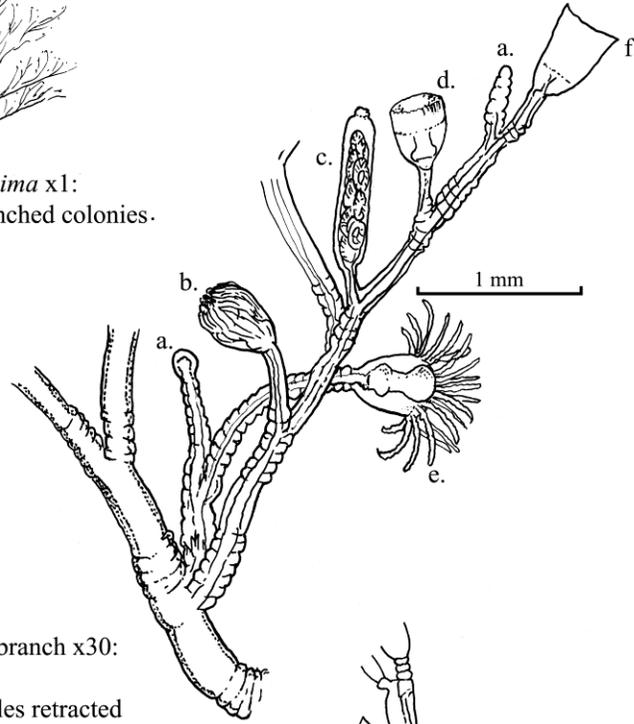
Body: Lacks nematophores (non-feeding defensive polyps) (Mills et al. 2007)

Pedicel: Stems are thread-like and often monosiphonic (consist of a single tube or row of cells) except sometimes near the base. Internodes of the stem are straight or curve very slightly (Mills et al. 2007). Each stem has many branches, which are ringed at the joints, alternate, and have short stalks



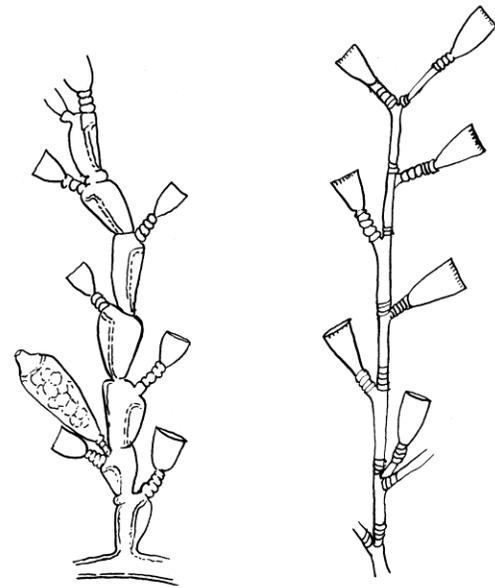
1. *Obelia longissima* x1:
white, many-branched colonies.

Obelia longissima



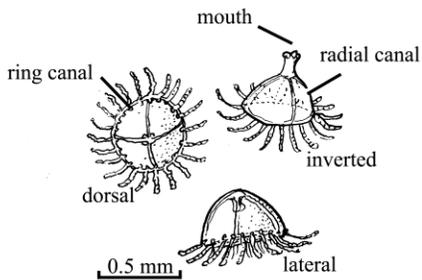
2. Closeup, single branch x30:

- a. buds
- b. hydranth, tentacles retracted
- c. gonotheca, showing medusae buds
- d. hydrotheca (covering young polyp)
- e. hydranth, tentacles extended
- f. empty hydrotheca



a. *O. geniculata*

b. *O. dichotoma*



3. Medusae x30:
actual diameter 0.5 mm.

4. Other species

(from Russell 1953, after Hincks 1868).

(Fig. 2). Stems hold many hydranths rather than just one (Mills et al. 2007).

Hydranth: The hydranth is covered by a theca (hydrothecae), which is campanulate (bell-shaped, hence family name) and deep enough to contain the hydranth when contracted. The margin is crenulate rather than cusped, and lacks an operculum (Mills et al. 2007). Each hydranth is on the end of a long, ringed pedicels (Fig. 2d, f).

Gonangium: The reproductive buds (gonotheca, gonangia) asexually produce medusae (Fig. 2c) (Ricketts et al. 1985). These buds are axillary (i.e., grow out of the angle between the stem and the hydrotheca). They are oval-shaped and smooth, with a raised central aperture (Parker et al. 1951) and a terminal collar (Mills et al. 2007).

Cnidae:

Possible Misidentifications

The family Campanulariidae includes leptomedusae possessing four radial canals, and lacking excretory pores and marginal or lateral cirri. The polyps in the family have a club or trumpet-shaped manubrium, and lack operculum. The genus *Obelia* includes species that have a nearly flat and eversible bell, a reduced velum, eight statocysts, and solid (rather than hollow) tentacles (Arai and Brinckmann-Voss 1980). Within the genus, the species look so similar (especially in the hydromedusa stage) that it is common for researchers to identify only to the genus level (Arai and Brinckmann-Voss 1980).

There are two very closely related species of *Obelia*: (Fig. 4)

Obelia geniculata has a central zig zag stem, thickened at the joints, while *O. longissima* has a much straighter and narrower stem. *Obelia geniculata* has a rather conical hydrothecae (as opposed to bell-shaped) that is only slightly longer than wide, and has plain margins rather than cusped (Fig. 4a). Colony size is also a difference; the maximum size of an *O. geniculata* colony is 2 cm (Cornelius 1975), much smaller than the 60 cm maximum of *O. longissima*. This size also gives *O. geniculata* a delicate white and fuzzy appearance (Kozloff 1983). The species are similar in that they both have ringed

branches and axillary gonothecae that are urn-shaped, with a raised center and a short ringed stalk. Their hydromedusae are also similar enough that they are often not identified past the genus level (Arai and Brinckmann-Voss 1980).

Obelia dichotoma is very similar to *O. longissima*. Both have slender and annulated stems, though *O. dichotoma* has curved internodes and is irregularly branched while *O. longissima* has a straight stem and is alternately branched. These are essentially the only differences. Both have hydrothecae that are broad, bell-shaped, with slightly sinuated margins; their gonothecae are axillar, slender, and smooth. They widen from the base, and end in a “raised, somewhat conical aperture” (Russell 1953) (Fig. 4b). No one has yet been able to definitively identify differences in the hydromedusae forms.

Other hydroids, which have stalks, and thecae within which their hydranths can be retracted (Fig. 2b) include those of the families Campanulinidae and Phialellidae (Rees and Hand 1975), which are very small and have tubular thecae with a pointed operculum. Other Campanularidae (bell-shaped hydrothecae) include *Phialidium sp.* and *Campanularia sp.* both of which have colonies of less than 2 cm in height, and are rarely branched.

The genus most closely related to *Obelia* is *Gonothyraea*, which does not release free medusae, but retains them within the gonotheca (Kozloff 1983).

Ecological Information

Range: The type locality is Belgium (Ralph 1957). The genus *Obelia* is found worldwide. *Obelia longissima* is found from Alaska to San Pedro, California (Ricketts et al. 1985).

Local Distribution: All three closely related species (*O. longissima*, *O. geniculata*, *O. dictotoma*) are found from northern California to Puget Sound, Washington; other species may be present as well, some of them introduced (Rees and Hand 1975).

Habitat: This is a frequent fouling organism, common in harbors (Mills et al. 2007), on docks, kelp, and floats in bays, and in eelgrass beds (Elkhorn Slough, CA) (Ricketts et al. 1985). Healthy colonies are found on exposed pilings, particularly where water is

clean and fast-moving. Medusae are found floating, probably not far from their hydroid parents. They probably are not light-dependent for vertical distribution (Parker and Haswell 1951). Polyps usually do not grow in pollution or direct sunlight (Ricketts et al. 1985).

Salinity: Collected at 30, though it can tolerate some fresh water (Ricketts et al. 1985). An Atlantic species, *O. bidentata* was found to have a wide distribution across the estuarine gradient, down to 0.5. *O. dichotoma* was found down to 12 (Cornelius 1975).

Temperature: Specimens have been found in cold and temperate waters; settling may occur in cooler temperatures during the year (Standing 1976).

Tidal Level: They are most abundant in mid-intertidal and just below, and have been found from low tide to 128 m (Mills et al. 2007).

Associates: The hydroid colonies serve as a good habitat for many epibionts. Some of these include caprellid and garnmarid amphipods; asellote isopods; copepods; diatoms; the sea slug *Eubranchus*; nudibranchs *Dendronotus frondosus* and *Phidiana crassicornis* (Bodega Bay); and pycnogonid *Halosoma veridintestinale*. The medusa form plays host to pycnogonid larvae of *Anaphia* (England). Despite both species' prevalence as fouling organisms, barnacle larvae cannot settle where *O. longissima* growth is heavy (Standing 1976).

Abundance: *Obelia longissima* is particularly common in harbors in northern California (Rees and Hand 1975), British Columbia, and Puget Sound (Arai and Brinckmann-Voss 1980; Ricketts et al. 1985). In the Strait of Georgia, it is collected from March to Sept., and common from April to June (Arai and Brinckmann-Voss 1980). Medusae are released primarily during summer, but also in smaller quantities throughout year (Ricketts et al. 1985). Medusa blooms and subsequent massive shoreline settlement are not common but do occasionally occur (Genzano et al. 2008).

Life-History Information

Reproduction: Like other hydroids, *O. longissima* has both a sexual reproductive cycle and an asexual one. In sexual reproduction, the medusae produce either eggs or sperm (dioecious). After the egg is

fertilized, it develops into a planula larva, which settles and becomes the polyp stage. In asexual reproduction, the gonangia of the polyp bud to form juvenile medusae. The production of medusae by the polyp may be tied to lunar periodicity: specifically, to the third week of the moon (Elmhirst 1925, in Russell 1953). The complete life cycle (swimming larvae to hydroid colony discharging medusae) takes one month (MacGinitie and MacGinitie 1968). Lab reared medusae are sexually mature six days after emergence (Russell 1953). *O. longissima* are present all year, but are most numerous in spring to late summer. Settling may correspond to low water temperatures (Standing 1976). Budding and release of medusae only occurs below 12° C (lab) (Haderlie et al. 1980).

Larva: The hydromedusae form produces planula larvae (Kozloff 1983). Planulae are usually oval or club-shaped and ciliated evenly all over their bodies. These larvae are non-feeding and free-swimming. They are armed with nematocytes, but lack an apical ciliary tuft and septa (see Fig. 3, Sadro 2001).

Juvenile: The juvenile medusa is about 0.5 mm in diameter had has 16-26 tentacles (Ricketts et al. 1985; Mills and Strathmann 1987). It lacks nematocysts on its lips (Boero et al. 2007).

Longevity: One generation (from newly-released larva to medusae-releasing hydroid) takes about one month (Ricketts et al. 1985).

Growth Rate: Because of the quick generation time and rapid hydroid growth, several generations are possible in a year (Ricketts et al. 1985). *Obelia dichotoma* grows to 2.5 mm in 19 days (from 1 mm) (Browne in Russell 1953). Growth is directly correlated with temperatures of 8-20° C (Haderlie et al. 1980).

Food: The medusa stage is considered a microphagous filter-feeder, especially as a juvenile (*O. dichotoma*) (Boero et al. 2007). Older individuals can sometimes consume crustaceans and their larvae, arrowworms, and small fish. The polyp stage primarily eats phytoplankton (diatoms and dinoflagellates), and secondarily eats detritus from macroalgae (De Rosa et al. 1999).

Predators: Opisthobranch *Eubranchus* and several nudibranch species eat hydroid buds (Ricketts et al. 1985; Mills et al. 2007). Other

hydrodmedusae prey upon the medusa stage (Arai and Jacobs 1980).

Behavior: The medusa is noted for its quick movements, and it is often found inverted (Fig. 3). Because of its flat bell, it uses bell-flapping rather than jet-propulsion to move through the water (see Fig. 2, Boero et al. 2007). This undulation is also how medusae maintain waterflow to their manubrium in order to continue filter-feeding. Juvenile medusae must flap their bells continuously (and thus feed continuously); they will undulate their bell while at the surface of the water to create waterflow while maintaining a single position (Boero et al. 2007). Medusae are bioluminescent, and are the source of the protein obelin (Ohmiya and Hirano 1996).

Bibliography

1. DE ROSA, S., A. MILONE, S. POPOV, and S. ANDREEV. 1999. Sterol composition of the Black Sea Hydrozoan, *Obelia longissima* (Pallas 1766). *Comparative Biochemistry and Physiology B: Biochemistry & Molecular Biology*. 123:229-233.
2. GENZANO, G., H. MIANZAN, L. DIAZ-BRIZ, and C. RODRIGUEZ. 2008. On the occurrence of *Obelia* medusa blooms and empirical evidence of unusual massive accumulations of *Obelia* and *Amphisbetia* hydroids on the Argentina shoreline. *Latin American Journal of Aquatic Research*. 36:301-307.
3. HADERLIE, E. C., C. HAND, and W. B. GLADFELTER. 1980. Cnidaria (Coelenterata): the sea anemones and allies, p. 40-75. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford.
4. KOZLOFF, E. N. 1983. *Seashore life of the northern Pacific coast*. University of Washington Press, Seattle.
5. MACGINITIE, G. E., and N. MACGINITIE. 1968. *Natural history of marine animals*. McGraw-Hill Book Co., New York.
6. MILLS, C. E., A. C. MARQUES, A. E. MIGOTTO, D. R. CALDER, and C. HAND. 2007. Hydrozoa: polyps, hydromedusae, and siphonophora, p. 118-168. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. C. Carlton (ed.). University of California Press, Berkeley.
7. MILLS, C. E., and M. F. STRATHMAN. 1987. Phylum Cnidaria, Class Hydrozoa, p. 44-71. *In: Reproduction and development of marine invertebrates of the northern Pacific coast: data and methods for the study of eggs, embryos, and larvae*. M. F. Strathman (ed.). University of Washington Press, Seattle, WA.
8. OHMIYA, Y., and T. HIRANO. 1996. Shining the light: the mechanism of the bioluminescence reaction of calcium-binding photoproteins. *Chemistry & Biology*. 3:337-347.
9. PARKER, T. J., O. LOWENSTEIN, C. F. COOPER, and W. A. HASWELL. 1951. *A textbook of zoology*. Macmillan and Co., London.
10. RALPH, P. M. 1957. New Zealand thecate hydroids. Part I. Campanulariidae and Campanulinidae. *Transactions of the Royal Society of New Zealand*. 84:811-854.
11. REES, J. T., and C. H. HAND. 1975. Class Hydrozoa, p. 65-84. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
12. RICKETTS, E. F., J. CALVIN, J. W. HEDGEPEETH, and D. W. PHILLIPS. 1985. *Between Pacific tides*. Stanford University Press, Stanford, CA.
13. RUSSELL, F. S. 1953. *The medusae of the British Isles*. University Press, Cambridge [Eng.].
14. SADRO, S. 2001. Cnidaria (Coelenterata), p. 13-23. *In: An identification guide to the larval marine invertebrates of the Pacific Northwest*. A. L. Shanks (ed.). Oregon State University, Corvallis.
15. SCHUCHERT, P. 2015a. Hydroidolina. *World Register of Marine*

- Species:
<http://www.marinespecies.org/aphia.php?p=taxdetails&id=19494>. [Accessed 7/17/15]. 2015.
16. —. 2015b. World Hydrozoa Database. <http://www.marinespecies.org/aphia.php?p=taxdetails&id=117389> [Accessed 2015-07-27]. 2015.
17. STANDING, J. D. 1976. Fouling community structure: effects of the hydroid *Obelia dichotoma* on larval recruitment. *In*: Coelenterate ecology and behavior. G. O. Mackie (ed.). Plenum Press, New York.

Updated 2015

C.D. Piazzola and T.C. Hiebert

Polyorchis penicillatus

Red-eye jellyfish, penicillate jellyfish

Phylum: Cnidaria
Class: Hydrozoa, Hydroidolina
Order: Anthoathecata, Capitata
Family: Corynidae

Taxonomy: *Polyorchis penicillatus* was originally identified as *Melicertum penicillatum* by Eschscholtz in 1829. It was re-described by Arai and Brinckmann-Voss in 1980 based on the lateral branches on its radial canals and its simple gonads. *P. minuta*, *P. montereyensis*, *P. campanula*, and *P. pinnatus* are all synonyms for *P. penicillatus* (Schuchert 2015c). Higher classification of this species has also undergone revision. The family Polyorchidae was determined to be a synonym of family Corynidae in 2010 (Schuchert 2015b). The order Hydroida was determined to be synonymous with subclass Hydroidolina in 2004 (Schuchert 2015a).

Description

General Morphology: The only known form of *P. penicillatus* is the gelatinous hydromedusa, with a deep bell and many tentacles. Within the bell are radial canals that run from the top of the bell to the bell margin, where they are connected by a ring canal (Fig. 1).

Medusa:

Size: *Polyorchis penicillatus* is higher than it is wide. Individuals can reach 60 mm in height (Mills et al. 2007) and average 20 mm in width (Ricketts et al. 1985).

Color: Most *P. penicillatus* are transparent white with purple-red eyespots. The color of the gonads (sausage-shaped and hanging from each radial canal, see Gonads) and other organs is variable and ranges from yellow brown to purple (Ricketts et al. 1985).

Body:

Bell: The bell is higher than it is wide. The membrane is thin, delicate, and not gelatinous.

Radial Canals: There are four radial canals, each with 15–25 pairs of short diverticula (blind side branches). The diverticula are longer than twice the width of the radial canal (Fig. 1) (Mills et al. 2007).

Ring Canals: The ring canal is simple (i.e., un-branching) and contains the tentacles. The ocelli are on extensions at the bases of the tentacles (Fig. 2).

Ocelli: Ocelli are pigment-cup eyespots suspended from the ring canal (fig. 2). The ocelli can measure gradients in light intensity (Martin 2002), which is thought to facilitate diel migration in *P. penicillatus*.

Mouth: The manubrium extends from a short, pronounced gelatinous gastric peduncle (Fig. 1), and is as long as the bell cavity. It has four oral lips densely armed with nematocysts that form a distinct marginal band (Fig. 1).

Tentacles: *Polyorchis penicillatus* can have up to 160 tentacles, set in a single whorl along the bell margin on the ring canal. The tentacles are not in clusters, and they are unbranched (Mills et al. 2007). The number of tentacles increases rapidly with age (Skogsberg 1948).

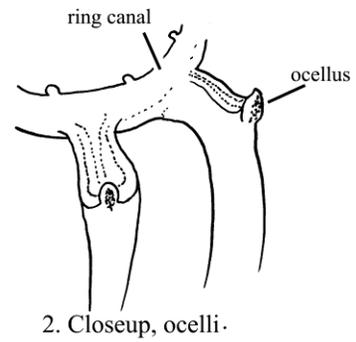
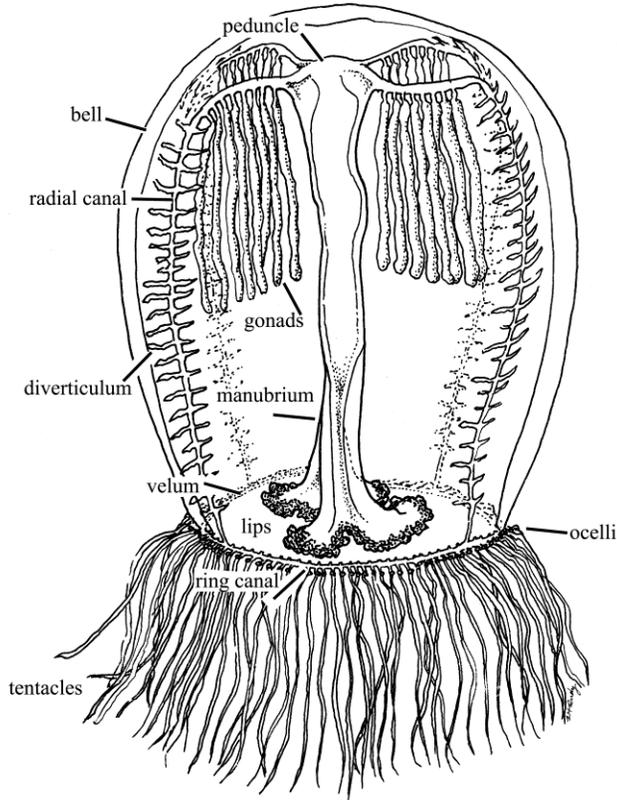
Velum: The velum is a thin layer inside the bell rim and contracts during swimming.

Gonads: There are four to eleven sausage-shaped gonads (with an average of eight) hanging from each radial canal as it joins manubrium (Fig. 1). They produce either eggs or sperm (dioecious).

Cnidae: Stinging cells, characteristic of all cnidarians, (Fig. 4) are found on the manubrium and tentacles. Each contains a poison sac and a stinging thread. According to Arai and Brinckmann-Voss (1980), the cnidoblasts (Fig. 3) are microbasic p-mastigophores in juveniles, and stenoteles and desmonemes in adults. However, there is variation in cnidoblast naming schemes between researchers.

Polyp: The polyp form of *P. penicillatus* is unknown. All attempts to raise *P. penicillatus* larvae in the lab have failed. It is possible that the polyp form is symbiotic on or in another organism (Mills et al. 2007).

Polyorchis penicillatus



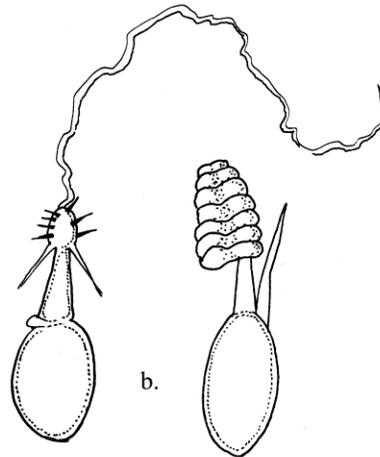
1. *Polyorchis penicillatus* x2:
actual size of bell 5 cm high four
radial canals, each with 15-25 pairs
diverticula; long manubrium;
nematocyst-banded lips; 4-11
sausage-shaped gonads; up to 160
tentacles on ring canal.



3. Cnidoblast.



4. Generalized
nematocysts:
a. undischarged.
b. exploded.



Possible Misidentifications

The family Polyorchidae includes bell-shaped anthomedusae with deep bodies. Juveniles lack a peduncle, which develops as they mature. Mature specimens also have four fringed oral lips, four radial canals, and gonads with either a sausage or spiral shape (Arai and Brinckmann-Voss 1980).

Two other species of Polyorchidae occur in our area. *Polyorchis haplus* is the smallest of the local Polyorchidae (up to 20 mm high), and has the fewest tentacles (up to 30). It also lacks knob-like diverticula on its radial canals (Mills et al. 2007). *Scrippisia pacifica*, the largest of the family (75 mm high), has a peduncle that reaches halfway down the bell (much longer than *P. penicillatus*). They also have many more tentacles (about 256) that are set in 7 whorls rather than one, and that can attach to the bell above, rather than just at, the radial canal.

Other tall, bell-shaped medusae are either very small (like *Aequorea*, this guide), or have greatly different tentacles or manubrium, as in *Coryne* or *Sarsia*. However, juveniles of *P. penicillatus* and *Sarsia bella* can be mistaken for one another. *Sarsia bella* has radial rows of two vertically aligned nematocyst patches while *P. penicillatus* has at least three patches per row. Additionally, the nematocysts are smaller in *S. bella* than they are in *P. penicillatus* (Brinckmann-Voss 2000).

Ecological Information

Range: The type locality is most likely San Francisco Bay. *Polyorchis penicillatus* has been found from the Aleutian Islands to the Sea of Cortez (Mills et al. 2007).

Local Distribution: Locally, *P. penicillatus* is found in the Coos Bay estuary.

Habitat: Medusae are found in the plankton near the surface of the water. They are often found in protected or shallow bays and around docks (Mills 1981; Mills et al. 2007), as well as in beds of *Zostera* species. (Mills and Strathmann 1987).

Salinity: Collected at salinities of 30.

Temperature: *Polyorchis penicillatus* is found in both cold (Vancouver, British Columbia, Canada) and temperate water

(San Francisco, California). However, it has been found as far south as the Gulf of California (Rees and Larson 1980; Mills 2001; Mills et al. 2007).

Tidal Level: Individuals are found throughout the water column, though they spend most of their time within several meters of the bottom.

Associates: *Polyorchis penicillatus* is parasitized by larvae of the sea spider *Achelia alaskensis* in Japan (Russel and Hedgpeth 1990) and by the Hyperiid amphipod *Hyperia medusarum* in Puget Sound, Washington (Towanda and Thuesen 2006).

Abundance: These are the most common large Anthomedusa in our area, but are speculated to be less abundant across their distribution, possibly due to increased urbanization of coastal regions as well as heavy take by scientists for research (Mills 2001).

Life History Information

Reproduction: Like other hydrozoans, *P. penicillatus* has a two-phased reproductive cycle, involving both asexual and sexual stages. Its sexual (medusa) stage is dioecious. Efforts to raise *P. penicillatus* in the lab have produced planula larvae, but they would not settle (Rudy pers. obs.). A single colony of *P. penicillatus* has been described, but was later identified as *Sarsia bella* (Brinckmann-Voss 1977, 2000). The medusae are highly fecund and produce 10,000 eggs a day for much of their lives (Mills 2001). One function of their diel migration could be to synchronize spawning locations. *Polyorchis penicillatus* spawn in the hour immediately after dark, a process that usually lasts less than ten minutes (Arkett 1984). The resulting eggs are transparent and 100 μm in diameter (Mills and Strathmann 1987).

Larva: *Polyorchis penicillatus* produces planula larvae. Planulae are usually oval or club-shaped and ciliated evenly all over their bodies. These larvae are non-feeding and free-swimming. They are armed with nematocytes, but lack an apical ciliary tuft and septa (see Fig. 3, Sadro 2001).

Juvenile: Juveniles have 24 small, distinct patches of cnidocysts on their exumbrella (the outer surface of the bell). There are six patches per quadrant, arranged in three rows

of two and spaced evenly over the surface of the bell. There is a red or a black ocellus on each tentacle bulb. They only have four tentacles, and the bell apex is rounded. They are only 1-2 mm in diameter and have been found around marina floats and over eelgrass beds (Mills et al. 2007).

Longevity: The longevity of *P. penicillatus* is unknown.

Growth Rate: Individuals grow rapidly in the spring, when food is abundant (Larson 1986).

Food: *Polyorchis penicillatus* eats large demersal crustaceans and other planktonic organisms, especially copepods, caprellid and gammarid amphipods, and tanaids (Arkett 1984). They feed in both the water column and on the bottom, using different methods for each (Mills et al. 2007). On the bottom, they perch on their tentacles and eat benthic organisms by touching the sediment with their manubrium. Sometimes, they will hop on the sediment, likely to stir up possible prey or move to a new location (Mills 1981, 2001). In the water column, they use "sink fishing" to find their prey. During sink fishing, the medusae extend their tentacles out from their bell and let the distal ends sink downward. They either maintain their position in the water column or sink slowly and catch prey with their tentacles. When a prey item touches a tentacle, the medusa will use that tentacle to bring the prey to the manubrium, though large prey sometimes require more tentacles; this process causes cessation in swimming and crumpling (Arkett 1984).

Predators: Eaten by the hydromedusa *Aequorea*, as well as fishes, sea anemones (*Urticina* sp., *Pachycerianthus* sp.) and crabs (*Cancer productus*). Most of their predators are benthic (Arkett 1985).

Behavior: Individuals exhibit a small diel migration (based on dusk and dawn) concomitant with demersal plankters. During the day, nearly all the medusae stay within a meter of the bottom, but at night they diffuse throughout the water column, though even then they usually stay within several meters of the bottom. This migration is heavily food-driven (Arkett 1984). They also exhibit a shadow response, in which rapid changes in light trigger a burst of swimming and tentacle contractions. Though this reaction was initially thought to be an escape method (Martin 2002), further research suggests it may be

related to their diel migration (Arkett 1985). Additionally, this response does not occur in young medusae (Arkett 1985).

Bibliography

1. ARAI, M. N., and A. BRINCKMANN-VOSS. 1980. Hydromedusae of British Columbia and Puget Sound. Canadian Bulletin of Fisheries and Aquatic Sciences. 204:1-192.
2. ARKETT, S. A. 1984. Diel vertical migration and feeding behavior of a demersal hydromedusan (*Polyorchis penicillatus*). Canadian Journal of Fisheries and Aquatic Sciences. 41:1837-1843.
3. —. 1985. The shadow response of a hydromedusan (*Polyorchis penicillatus*): Behavioral mechanisms controlling diel and ontogenic vertical migration. Biological Bulletin. 169:297-312.
4. BRINCKMANN-VOSS, A. 1977. The hydroid of *Polyorchis penicillatus* (Eschscholtz) (Polyorchidae, Hydrozoa, Cnidaria). Canadian Journal of Zoology. 55:93-96.
5. —. 2000. The hydroid and medusa of *Sarsia bella* sp nov (Hydrozoa, Anthoathecatae, Corynidae), with a correction of the "life cycle" of *Polyorchis penicillatus* (Eschscholtz). Scientia Marina. 64:189-195.
6. LARSON, R. J. 1986. Seasonal changes in the standing stocks, growth rates, and production rates of gelatinous predators in Saanich Inlet, British Columbia. Marine Ecology Progress Series. 33:89-98.
7. MARTIN, V. J. 2002. Photoreceptors of cnidarians. Canadian Journal of Zoology. 80:1703-1722.
8. MILLS, C. E. 1981. Diversity of swimming behaviors in hydromedusae as related to feeding and utilization of space. Marine Biology. 64:185-189.
9. —. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia. 451:55-68.
10. MILLS, C. E., A. C. MARQUES, A. E. MIGOTTO, D. R. CALDER, C. HAND,

- J. T. REES, S. H. D. HADDOCK, C. W. DUNN, and P. R. PUGH. 2007. Hydrozoa: polyps, hydromedusae, and siphonophora, p. 118-167. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley.
11. MILLS, C. E., and M. F. STRATHMAN. 1987. Phylum Cnidaria, Class Hydrozoa, p. 44-71. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast: data and methods for the study of eggs, embryos, and larvae. M. F. Strathman (ed.). University of Washington Press, Seattle, WA.
12. REES, J. T., and R. J. LARSON. 1980. Morphological variation in the hydromedusa genus *Polyorchis* on the west coast of North America. *Canadian Journal of Zoology*. 58:2089-2095.
13. RICKETTS, E. F., J. CALVIN, J. W. HEDGEPEETH, and D. W. PHILLIPS. 1985. *Between Pacific tides*. Stanford University Press, Stanford, CA.
14. RUSSEL, D. J., and J. W. HEDGPETH. 1990. Host utilization during ontogeny by two pycnogonid species (*Tanystylum duospinum* and *Ammothea hilgendorfi*) parasitic on the hydroid *Eucopeella everta* (Coelenterata, Campanulariidae). *Bijdragen Tot De Dierkunde*. 60:215-224.
15. SADRO, S. 2001. Cnidaria (Coelenterata), p. 13-23. *In*: An identification guide to the larval marine invertebrates of the Pacific Northwest. A. L. Shanks (ed.). Oregon State University, Corvallis.
16. SCHUCHERT, P. 2015a. Hydroidolina. Vol. 2015, World Register of Marine Species: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=19494>. [Accessed 7/17/15].
17. —. 2015b. Polyorchidae Agassiz, 1862. Vol. 2015. P. Schuchert (ed.), World Register of Marine Species: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=266974>. [Accessed 7/17/2015].
18. —. 2015c. *Polyorchis penicillatus* (Eschscholtz, 1829). Vol. 2015. P. Schuchert (ed.), World Register of Marine Species: <http://marinespecies.org/aphia.php?p=taxdetails&id=290843>. [Accessed 7/17/2015].
19. SKOGSBERG, T. 1948. A systematic study of the family Polyorchidae (Hydromedusae). *Proceedings of the California Academy of Sciences*. 4:101-124.
20. TOWANDA, T., and E. V. THUESEN. 2006. Ectosymbiotic behavior of *Cancer gracilis* and its trophic relationships with its host *Phacellophora camtschatica* and the parasitoid *Hyperia medusarum*. *Marine Ecology Progress Series*. 315:221-236.

Updated 2015

C.D. Piazzola and L. Hiebert

Ectopleura crocea

A tubular hydroid

Phylum: Cnidaria

Class: Hydrozoa, Hydroidolina

Order: Anthoathecata, Aplanulata

Family: Tubulariidae

Taxonomy: *Ectopleura crocea* was originally described by Agassiz, 1862 as *Parypha crocea*, though it was soon after classified as *Tubularia crocea* (Allman 1871). The primary synonyms are *T. crocea* and *Pinauy crocea* (Mills et al. 2007). There has been much debate about the appropriate genus for this species, but *Ectopleura crocea* is now generally accepted (van der Land et al. 2001; Schuchert 2015). Additional synonyms include *Tubularia ralphi*, *T. gracilis*, *T. australis*, and *T. warreni* (Schuchert 2010).

Description

General Morphology: The only form of *E. crocea* is the large, colonial polyp. Each polyp has a stem (hydrocaulus) covered in a rigid perisarc and an athecate hydranth with a mouth (manubrium), stomach, tentacles, and gonophores (Figs. 1, 2).

Medusa: The medusa is not free-swimming (Ricketts et al. 1985); though it is biologically similar to other free-swimming hydromedusa, it is entirely retained in the tissue of the gonophore (Kozloff 1983).

Polyp:

Size: The colony grows in large bushy clusters up to 15 cm (Ricketts et al. 1985). Stems grow to 2 cm long, and "flowers" (the hydranth) are up to 1 cm when extended. The genus *Ectopleura* contains species that are considered the largest athecate hydroids (Kozloff 1974).

Color: The hydrocaulus is white to light tan, the feeding tentacles (proximal and distal) are transparent white, the gonophores are light pink and dark coral, and the manubrium is a pale yellow-orange. The organism's dominant color comes from the pink to red hydranths (Ricketts et al. 1985).

Body:

Pedichel: The hydrocaulus is unbranched, crooked, and covered with fine "hairs" (diatoms). The stiff perisarc extends to the base of the hydranth (Mills et al. 2007).

Hydranth: The hydranth lacks a theca. The manubrium is surrounded by a whorl of tentacles, is simple, and circular (Fig. 3).

Gonophore: The gonophores each contain an abortive medusae, or gonomedusae. They are in clusters on stalks (racemes) between the two whorls of tentacles (Fig. 3). Within the gonophores develop the planulae larvae, which leave the gonophore but remain in close association with the polyp (Kozloff 1983). Female gonophores have short distal crests (Mills et al. 2007), with 4-8 flattened bladelike tentacles at the apical end (Kozloff 1987). Male gonophores lack tentacles (Mills and Strathmann 1987).

Cnidae:

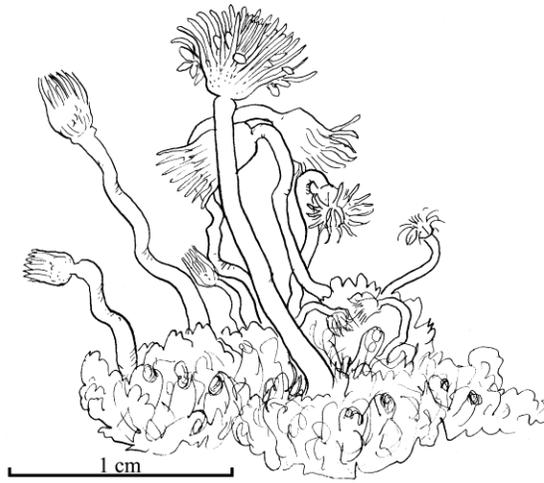
Tentacles: Tentacles are filiform (thread-like), simple, and in two whorls (oral and aboral, Mills et al. 2007). The proximal, or aboral, whorl consists of long, extended feeding tentacles at the base of the hydranth, while the distal, or oral, whorl has short tentacles usually contracted around mouth (Figs. 2, 3). There are similar numbers of distal and proximal tentacles (Kozloff 1987). Older specimens have more tentacles than young ones; juveniles will have only 10 proximal tentacles.

Possible Misidentifications

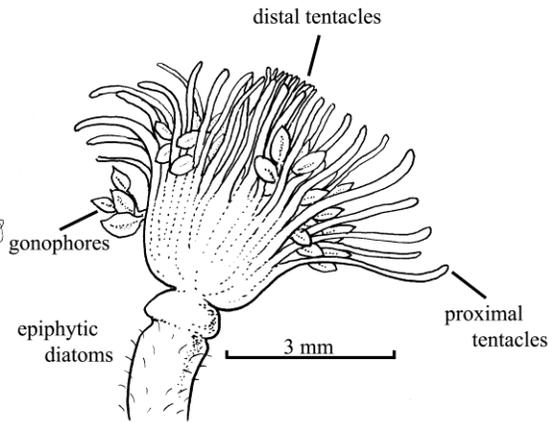
The family Tubulariidae is composed of hydroids with a thick perisarc and stolons (ground-level shoots connecting branches). Species in this family have at least two tentacle whorls and gonophores between the oral and aboral whorls. The medusae in this family can be either free-swimming or retained, have four radial canals, a simple mouth, and few tentacles. Divisions of the family into its genera are based on presence of stolons, texture of the stem, origin of the perisarc, and morphology of the medusa stage (Schuchert 2012).

The genus *Ectopleura* is composed of hydroids with only two tentacle whorls, one

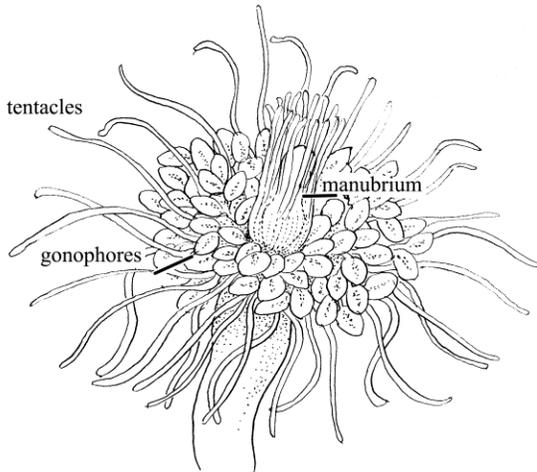
Ectopleura crocea



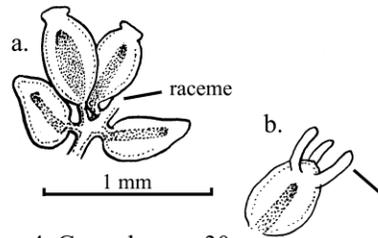
1. *Pinauy crocea* colony x4:
actual polyp height c. 2 cm.



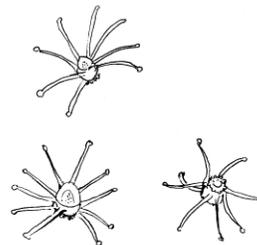
2. Hydranth x10:
actual diameter 3mm
two whorls of tentacles, distal and proximal;
gonophores between whorls.



3. Hydranth, extended x10.



4. Gonophores x30:
a. showing racemes (stems)
b. with developing marginal lappets.



5. Actinulae x30.

oral and one aboral. The perisarc originates below the connection between the hydranth and stem, and ends at the base of the hydranth. The stem is a hollow tube with 0-5 ridges. Stolons are present. The medusae can be free-swimming or retained (Schuchert 2012).

The other common local species of *Ectopleura*, *E. marina*, is a small, solitary athecate (without a cup-like theca) hydroid of the outer coast. Its stalk is usually about 2.5 cm long, it has fewer distal tentacles than proximal ones, and it is less showy than *E. crocea*, as it does not occur in clumps as the latter does. While *E. crocea* branches extensively from its base, *E. marina* does not (Kozloff 1983).

Other athecate hydroids often have some capitate (knobbed) tentacles as adults, i.e. *Cladonema*, *Hydrocoryne*. Of those with only threadlike tentacles, some like *Hydractinia* and *Eudendrium* have only a single whorl of tentacles, not two whorls as in *Ectopleura crocea*. Others, such as *Turritopsis* and *Clava* have tentacles in scattered patterns rather than in whorls (Rees and Hand 1975).

The species *Ectopleura larynx* looks similar to *E. crocea*, but is not found in Oregon.

Ecological Information

Range: The type locality is Boston Harbor (Agassiz 1862). This species is native to the northern Atlantic Ocean, and was introduced to the Pacific via ship bottoms (Mills et al. 2007). It has been found on both sides of the Atlantic and from the Gulf of Alaska to southern California, and thrives in northern temperate oceans (Ricketts et al. 1985).

Local Distribution: This species is common in Oregon and California estuaries, and seems to be a more northern species. In the Coos Estuary, it has been found in South Slough, Charleston, and Fossil Point.

Habitat: One of the most prominent fouling organisms, *E. crocea* is often found on undersides of floating docks, boat bottoms, and wharf pilings (Ricketts et al. 1985, Mills et al. 2007). It thrives in cold water with good movement. In the lab, it is not bothered by strong light (Mackie 1966). It is one of the invertebrate organisms most resistant to poisons, such as copper (Barnes in Pyefinch and Downing 1949). It lives in the low

intertidal and down to 40 m (Mills et al. 2007), and is always attached to solid substratum rather than mud or sand (Kozloff 1987).

Salinity: Collected at 30.

Temperature: Specimens respond badly to warm water in the lab and will lose hydranths. Regression occurs with summer temperatures (Mackie 1966). *Ectopleura crocea* is usually found at temperatures above 18°C, but can be kept in laboratories at 14° C (Mills and Strathmann 1987).

Tidal Level: Low intertidal; subtidal to 40m (Haderlie et al. 1980)

Associates: On floating docks, the colonial *Ectopleura crocea* and its substrate constitute a rich microecosystem. Some of the most common epibionts are suctorian protozoans, diatoms (especially in fall, darkening stems) (Pyefinch and Downing 1949), caprellid and tube-building amphipods, isopods, copepods, and mussels. *Ectopleura crocea* has, however, become a nuisance to mussel-growing aquaculturists. The hydroid will foul on juvenile mussels, restricting their growth by impeding their ability to filter water and by competing for food. Additionally, *E. crocea* will eat incoming mussel larvae, which decrease settlement rates in commercial mussel facilities (Fitridge and Keough 2013, Fitridge 2011). A pycnogonid, *Anoplodactylus erectus*, is parasitic in the digestive tract of *Ectopleura crocea* in southern California, distending the polyps abnormally (Ricketts et al. 1985, Rees and Russell 1937). Some amphipods (*Stenothoe*) are immune to *E. crocea*'s nematocysts (Mackie 1966). The colonies also provide a habitat for the egg masses of some benthic opisthobranchs (Mills et al. 2007).

Abundance: Colonies can be quite dense under the right conditions of water and currents. In ideal conditions, actinulae are released August-October and February-March (Elkhorn Slough, CA), and, in less favorable environments, August-November (Mills and Strathmann 1987). In warmer waters the species shows a seasonal pattern of high abundance during cool months and low abundance during warm; it has also been decreasing in abundance since about 1980, likely due to increasing ocean temperatures (Mediterranean Sea) (Di Camillo et al. 2013).

Life-History Information

Reproduction: The polyps can reproduce both sexually and asexually. In asexual reproduction, new hydranths can grow from the stolons (horizontal shoots at the base of each hydrocaulus). *Ectopleura crocea* is dioecious, so each colony is entirely male or entirely female during sexual reproduction. The gonophores correspond to the medusae stage in other hydroids, and so are called gonomedusae. In the summer, male gonomedusae release their sperm, which are attracted to the female gonomedusae and their eggs (Ricketts et al. 1985). Within the gonomedusae develop the planulae, which leave the gonomedusae but remain in close association with the polyp (Kozloff 1983) and metamorphose into the actinulae (Fig. 5). Actinulae are mobile, crawling larvae shaped like little polyps with the characteristic whorls of tentacles (Kozloff 1983). To develop into the adult polyp form, the actinulae moves away from its “parent” polyp and settles on the nearby substratum (Kozloff 1983). There is no swimming stage. One polyp can produce over 100 gonomedusae (not simultaneously) (Miller 1976). Gonomedusae most distal on the racemes (stalks) mature soonest (Mackie 1966). Mature male gonomedusae are white, while immature have a red stripe. The mechanism for spawning and larvae release is not known (Miller 1976), but possibly could be due to a change in light intensity and water speed (Pyefinch and Downing 1949). In one area, only one species of *Ectopleura* will be sexually active at a time (Miller 1976).

Larva: Actinula larvae are the larval stage; these larvae attach to substrate and become a new polyp. They can have up to 10 capitata (knobbed) tentacles containing nematocysts; visible inside are the manubrium and distal tentacle buds (Fig. 5). In *E. larynx*, tentacles can vary from 6 to 13, though most have 10 (Pyefinch and Downing 1949).

Juvenile: Juveniles develop from settled actinulae, often near the “parent” polyp. They have fewer tentacles and will develop more as they age.

Longevity: Unknown

Growth Rate: It takes two weeks for juveniles to reach maturity, and takes 6-8 days to go from ripe female gonads to the liberation of viable actinulae (Mackie 1966).

Time from settlement of actinulae to first generation of new larvae takes 24 days (Pyefinch and Downing 1949). The stolon growth rate is a steady 1 mm/day (Mackie 1966). Settlement of actinulae begins after about 24 hours (Pyefinch and Downing 1949). This species is easily grown in the lab.

Food: The polyps eat copepods, chaetognaths, portunid zoeae, small mysids, siphonophores, eudoxids, and salps; they reject pteropods and pycnogonids.

Predators: The polyps are eaten by pycnogonids and nudibranchs (Mills et al. 2007; Pyefinch and Downing 1949; Strathmann 1987).

Behavior: While each polyp is technically an individual organism, behavior tends to be on a colonial scale (Pyefinch and Downing 1949). Hydranths will fall off (autotomize) in unfavorable conditions (Ricketts et al. 1985). The behavior of the actinula stage differs the most from other hydroids (see behavior in Reproduction above).

Bibliography

1. AGASSIZ, L. 1862. Contributions to the natural history of the United States of America. IV Discophorae. Hydroidae. Homologies of the Radiata. Little Brown, Boston.
2. ALLMAN, G. J. 1871. A Monograph of the gymnoblastic or tubularian hydroids. Ray Society, London.
3. DI CAMILLO, C. G., G. GIORDANO, M. BO, F. BETTI, M. MORI, S. PUCE, and G. BAVESTRELLO. 2013. Seasonal patterns in the abundance of *Ectopleura crocea* (Cnidaria: Hydrozoa) on a shipwreck in the Northern Adriatic. *Marine Ecology*. 34:25-32.
4. FITRIDGE, I. 2011. The ecology of hydroids (Hydrozoa: Cnidaria) in Port Phillip Bay, Australia, and their impacts as fouling species in longline mussel culture. PhD. University of Melbourne.
5. FITRIDGE, I., and M. J. KEOUGH. 2013. Ruinous resident: the hydroid *Ectopleura crocea* negatively affects suspended culture of the mussel *Mytilus galloprovincialis*. *Biofouling*. 29:119-131.
6. HADERLIE, E.C., C. HAND, and W.B. GLADFELTER. 1980. Cnidaria

- (Coelenterate): the sea anemones and allies, p.40-75. In: Intertidal invertebrates of California. R. H. Morris, D. P. Abbot, and E.C. Haderlie (eds.). Stanford University Press, Stanford, California.
7. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
 8. —. 1983. Seashore life of the northern Pacific coast. University of Washington Press, Seattle.
 9. —. 1987. Marine invertebrates of the Pacific Northwest. University of Washington Press, Seattle and London.
 10. MACKIE, G. O. 1966. Growth of the hydroid *Tubularia* in culture, p. 397-412. In: The Cnidaria and their evolution: the proceedings of a symposium held at the Zoological Society of London on 3 and 4 March 1965. W. J. Rees (ed.). Academic Press, London.
 11. MILLER, R. L. 1976. Some observations on sexual reproduction in *Tubularia*, p. 299-308. In: Coelenterate ecology and behavior: [selected papers]. G. O. Mackie (ed.). Plenum Press, New York.
 12. MILLS, C. E., A. C. MARQUES, A. E. MIGOTTO, D. R. CALDER, C. HAND, J. T. REES, S. H. D. HADDOCK, C. W. DUNN, and P. R. PUGH. 2007. Hydrozoa: Polyps, Hydromedusae, and Siphonophora, p. 118-167. In: The Light and Smith Manual. J. T. Carlton (ed.). University of California Press, Berkeley.
 13. MILLS, C. E., and M. F. STRATHMAN. 1987. Phylum Cnidaria, Class Hydrozoa, p. 44-71. In: Reproduction and development of marine invertebrates of the northern Pacific coast: data and methods for the study of eggs, embryos, and larvae. M. F. Strathman (ed.). University of Washington Press, Seattle, WA.
 14. PYEFINCH, K. A., and F. S. DOWNING. 1949. Notes on the general biology of *Tubularia larynx* Ellis and Solander. Journal of the Marine Biological Association of the United Kingdom. 28:21-43.
 15. REES, J. T., and C. H. HAND. 1975. Class Hydrozoa, p. 65-84. In: Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
 16. REES, W. J., and F. S. RUSSELL. 1937. On rearing the hydroids of certain medusae, with an account of the methods used. Journal of the Marine Biological Association of the United Kingdom. 22:61-82.
 17. RICKETTS, E. F., J. CALVIN, AND J.W. HEDGEPEETH. 1985. Between Pacific tides. Stanford University Press, Stanford.
 18. SCHUCHERT, P. 2010. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 2. Revue Suisse De Zoologie. 117:337-555.
 19. —. 2012. North-west European athecate hydroids and their medusae. Field Studies Council Publications, Telford, UK.
 20. —. 2015. World Hydrozoa Database. Accessed at <http://www.marinespecies.org/hydrozoa> on 2015-10-06.
 21. STRATHMAN, M. F. 1987. Phylum Mollusca, Class Gastropoda, Subclass Opisthobranchia, p. 268-302. In: Reproduction and development of marine invertebrates of the northern Pacific coast: data and methods for the study of eggs, embryos, and larvae. M. F. Strathman (ed.). University of Washington Press, Seattle, WA.
 22. VAN DER LAND, J., W. VERVOORT, S. D. CAIRNS, and P. SCHUCHERT. 2001. Hydrozoa, p. 112-122. In: European register of marine species: a check-list of the marine species in Europe and a bibliography of guides to their identification. M. J. Costello, C. S. Embrow, and R. J. White (eds.). Muséum National d'Histoire Naturelle, Paris.

Updated 2015

C.D. Piazzola and T.C. Hiebert

Anthopleura artemisia

Buried anemone, moonglow anemone

Phylum: Cnidaria

Class: Anthozoa, Hexacorallia

Order: Actiniaria, Nynantheae, Thenaria

Family: Endomyaria, Actiniidae

Taxonomy: *Anthopleura artemisia* was originally described by Pickering in Dana (1846) as *Actinia artemisia*. The subclass Zoantharia has been synonymized with Hexacorallia (Hoeksema 2015).

Description

Medusa: No medusa stage in Anthozoans.

Polyp:

Size: Most solitary polyps are around 2.5 cm in diameter, and can extend 6-7 cm long. The specimen used for this description was 2 cm long, with a 2.5 cm crown diameter and 1.5 cm column diameter. The column may have to extend 15-20 cm from its attachment to the sediment surface, and a fully expanded crown and tentacles can be 5 cm in diameter (Kozloff 1983).

Color: The oral disc can be red, brown, gray, or black, and can have solid or concentric patterns. The specimen used for this description had a brown disc with tan spots and a light tan mouth. Tentacles can be brightly colored and/or patterned with nearly every color (red, white, black, blue, or orange, Hand 1975; pink and green, Ricketts et al. 1985; white bands on gray, brown, black, or green background, Kozloff 1974). The specimen used for this description had "day glow" and pink tentacles and pink spots on oval disc. The discs can also be semitransparent (Ricketts et al. 1985). The top third of the column is black, brown, or gray shading to white or pink at the bottom third (the specimen used for this description was gray). Verrucae on the collar tend to be white-tipped (Hand 1955). Mesentery insertions can be visible on the bottom 3rd of column, showing as vertical white lines (not on the specimen used in this description). Acrorhagi are white (fig. 2) (Fautin and Hand 2007).

Body: The polyp can have a very extended column (not figured), with tubercles (verrucae) near the top. Its tentacles are slender and tapering. They are extensions of the gut cavity, and so are hollow. The anemone has a broad flat oral

disc, a prominent collar, and acrorhagi (spherules). *Anthopleura artemisia* can also contract into a crevice with only its crown showing. When contracted, it forms a low round-topped pillar (fig. 1) (Hand 1955). The column has a groove below the tentacles (fosse) covered by a distinct fold (parapet or collar). Adherent shell and debris are typical of this solitary species.

Column: The column can extend to 5 times the diameter. It has a well-developed collar and longitudinal rows of verrucae on uppermost (distal) third of column (fig. 1). There are rarely any verrucae on proximal 3rd of column (Fautin and Hand 2007).

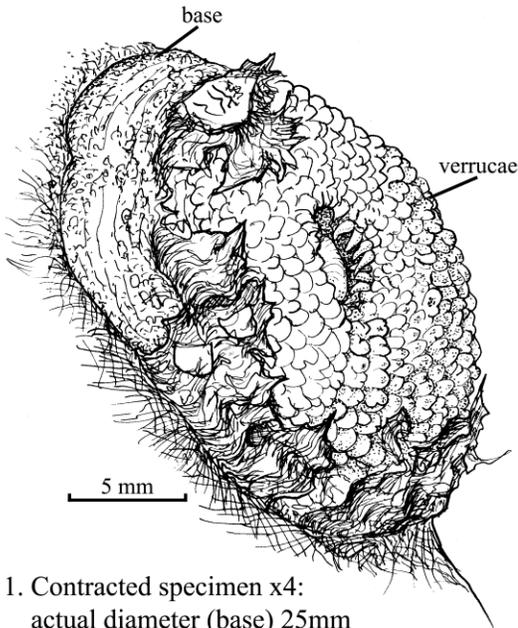
Collar: The parapet is well-developed and separated from tentacles by a deep fosse (groove) in which there are acrorhagi (spherules). The collar is covered with compound verrucae (fig. 3).

Oral Disc: The oral disc is a large central area without tentacles on the top of the column, and sometimes has a radial pattern. It is broad, usually flat, and about 1.5 times the column diameter when expanded. It has radial lines (mesenterial insertions) (fig. 2). Its lips are not ribbed and do not protrude above the disc surface. They usually have siphonglyphs (ciliate grooves). The mouth is commonly an elongate slit (Fig. 2).

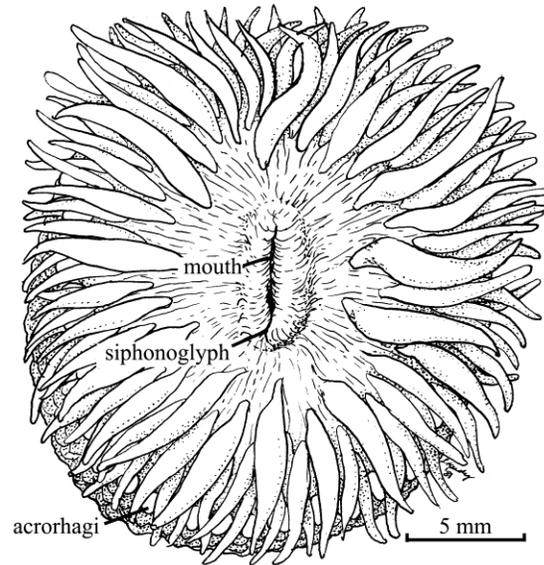
Tentacles: There are numerous slender, tapering tentacles. They are about half as long as the oral disc diameter. There are rarely more than 5 orders (rows) (Hand 1955). Arrangement is sometimes irregular due to longitudinal fission. There are no acontia (thread-like defensive structures expelled through column wall).

Mesenteries: Mesenteries are interior vertical partitions. There are up to 24 pairs in some adults. They are often irregular due to asexual longitudinal fission. Mesenterial insertions are often visible as white lines on the proximal third of the column in elongated specimens (not shown).

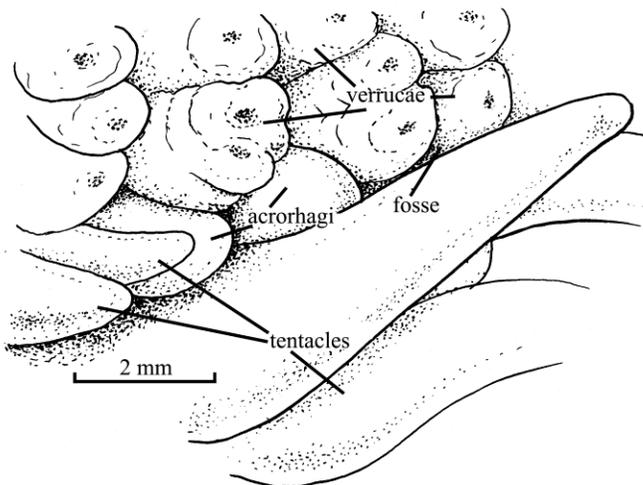
Anthopleura artemisia



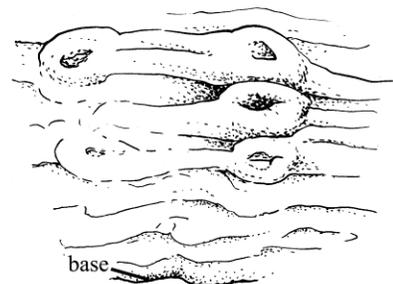
1. Contracted specimen x4:
actual diameter (base) 25mm
algae, shell adhere to verrucae on upper third,
sand particles near base; column gray;
many verrucae on upper third, sparse on middle
third, none near base.



2. *Anthopleura artemisia* crown x4:
width 25 mm; brightly colored tentacles, slender,
tapering, about 5 rows; broad oral disc;
lips not grooved, mouth a long slit; 1-3 siphonoglyphs.
acrorhagi: round, white, under tentacles.



3. Verrucae, acrorhagi (collar) x12:
verrucae compound; acrorhagi round, white,
in single row in fosse under tentacles.



4. Verrucae, mid-column x12:
simple, sparsely spaced; none near base.

Pedal Disc: The pedal disc attaches the column firmly to the substrate. It is circular to irregular, and is often wider than the column. There is no physa (bulb) at the base.

Cnidae: Cnidae are tiny stinging cells. *Anthopleura artemisia* has many different kinds, varying in size, distribution from other species (not shown).

Acrorhagi: Also known as spherules, these fighting tentacles are round, hollow bodies covered with nematocysts. They are inconspicuous structures in the fosse, just under the tentacles (fig. 2, 3) (Hyman 1940).

Verrucae: These are rounded, wart-like tubercle structures that pebble the column. They are well-developed and arranged in longitudinal rows on upper third of column, and sparsely spaced and solitary on the middle third of column; there are usually none on lowest third of column (Hand 1955). They are also on the collar, where they are compound, with 3-6 vesicles each (fig. 3). Verrucae are adherent, and collect a layer of shells and debris for protection (MacGinitie and MacGinitie 1968). They also contain cinclides (pores) (see fig. 4, *A. elegantissima*). Those near the acrorhagi are sometimes white-tipped.

Possible Misidentifications

There are other more common estuarine anemones (*Metridium*, *Diadumene*, etc.), but none of them have acrorhagi inside the fosse at the collar edge, or adherent tubercles on the column. *Anthopleura* species have both of these, as well as a well-developed pedal disc (base), and a flat broad oral disc with a clear central area.

Anthopleura xanthogrammica is usually an open coast species, large, green solitary and unicolored; its column is completely covered with verrucae (they are not in rows). It is found occasionally in the lower reaches of the most marine estuaries.

Anthopleura elegantissima, the aggregating anemone, can be solitary, like *A. artemisia*, and is often found in like habitats, i.e., rock substrate with sand and mud over the rock. *Anthopleura elegantissima* has verrucae in longitudinal rows on the entire column, not just on the upper part; the column is green or whitish, not black or gray fading to pinkish. The tentacles in *A. elegantissima* are pink,

white, purple, blueish or green, not brightly colored red, orange or patterned, as in *A. artemisia*. *Anthopleura elegantissima*, when solitary, is usually larger than *A. artemisia*, which never has symbiotic algae in its endoderm. *Anthopleura artemisia* is the only species of the genus whose verrucae do not extend down to the base.

A third species of *Anthopleura*, *A. sola*, is very similar in appearance to *A. elegantissima*. The primary difference between the two is that *A. elegantissima* is clonal while *A. sola* is solitary. Though *A. sola* is not found locally, there are many examples in the literature of *A. sola* being misclassified as *A. elegantissima*, and some examples of it being misclassified as *A. artemisia* (Pearse and Francis 2000).

Retracted *A. artemisia* can be confused with *Metridium*, for their bright tentacles are hidden and they are plain white or green-gray (Ricketts et al. 1985).

Ecological Information

Range: The type localities are Discovery Harbor, Puget Sound, and the northwest coast of North America (Pickering in Dana 1846). The range is Alaska to southern California (Ricketts et al. 1985), and possibly Japan (Hand 1955).

Local Distribution: In Coos Bay, they can be found in high abundance at Pigeon Point.

Habitat: In estuaries, *Anthopleura artemisia*'s column is often buried in mud or sand in a crevice or pholad burrow, with only the crown exposed, while the base is attached to solid substrate beneath the softer sediment. It withdraws into its burrow when disturbed or at low tide. It can also be found on pilings, floats, and the open coast. It is solitary on open coasts, lives in groups in estuaries, and is individually attached to stones buried in the muddy sand (Fautin and Hand 2007).

Salinity: Collected at 30.

Temperature: 8° C to 13° C (Anderson 2000).

Tidal Level: Distribution centers around mean lower low water, but specimens are also found occasionally quite a bit higher (Hand 1955).

Associates: Though there is some debate on the topic (Kozloff 1983), it is unlikely that *A. artemisia* contains the symbiotic green algae (zoochlorellae) and dinoflagellates

(zooxanthellae) that are found in other *Anthopleura* species (Geller and Walton 2007; Weis et al. 2005). Copepods sometimes live on the anemone's column (Lønning and Vader 1984).

Abundance: This species is less abundant than *A. elegantissima* in most places (Smith and Potts 1987).

Life-History Information

Reproduction: There are both sexual and asexual reproductive cycles. Individual anemones are sexually dioecious. Gonads are borne on directive mesenteries attached to siphonoglyphs. This species has been witnessed in mass spawning events during low tide, in which nearly every individual in the area releases their gametes in broadcast spawning (Weis et al. 2005). Asexually, specimens can divide by longitudinal fission.

Larva: This species produces feeding planula larvae with similar development to *A. elegantissima* (Weis et al. 2005). They are ovaloid to cylindrical, covered in cilia, and have an apical tuft. They actively swim using the cilia on their apical tuft (Sadro 2001).

Juvenile:

Longevity: Unknown.

Growth Rate: Unknown.

Food: *Anthopleura artemisia* is a carnivorous stationary hunter in the tidepools (Niesen 2007) that uses tentacles to capture prey (Ricketts et al. 1985). It primarily eats small crustaceans.

Predators: This anemone is not one of the preferred foods of coelenterate predator *Aeolidia papillosa* (Waters 1975). It is eaten by occasionally by *A. papillosa*, and is likely prey to other nudibranchs and small fish (Ottaway 1977).

Behavior: They will retract completely into their "burrow" when disturbed. They will display aggressive behavior when brought into contact with members of the same species as well as other anemone species. This behavior is similar to the aggressive response in *A. elegantissima*, in which the acrohagi inflate and attack neighboring anemones (Francis 1973).

Bibliography

1. ANDERSON, R. C. 2000. Sea anemones of the north-eastern Pacific: the flowers of the sea. International Zoo Yearbook. 37:321-330.
2. FAUTIN, D. G., and C. HAND. 2007. Anthozoa, p. 173-184. *In*: The Light and Smith Manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley.
3. FRANCIS, L. 1973. Intraspecific aggression and its effect on the distribution of *Anthopleura elegantissima* and some related sea anemones. Biological Bulletin. 144:73-92.
4. GELLER, J. B., and E. D. WALTON. 2001. Breaking up and getting together: evolution of symbiosis and cloning by fission in sea anemones (genus *Anthopleura*). Evolution. 55:1781-1794.
5. HAND, C. H. 1955. The sea anemones of central California. Part II. The endomyarian and mesomyaroon anemones. Wasmann Journal of Biology. 13:37-99.
6. —. 1975. Class anthozoa, p. 85-93. *In*: Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
7. HOEKSEMA, B. 2015. Hexacorallia. Vol. 2015, World Register of Marine Species: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=1340>. [Accessed 9/23/2015].
8. HYMAN, L. H. 1940. The Invertebrates: Protozoa through Ctenophora. McGraw-Hill, New York, London.
9. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
10. —. 1983. Seashore life of the northern Pacific coast. University of Washington Press, Seattle.
11. —. 1987. Marine invertebrates of the Pacific Northwest. University of Washington Press, Seattle.
12. LONNING, S. V., W. 1984. Sibling species of *Doridicola* (Copepoda:

- Lichomolgidae) from California sea anemones: biology and host specificity. *Journal of Experimental Marine Biology and Ecology*. 77:99-135.
13. MACGINITIE, G. E., and N. MACGINITIE. 1968. Natural history of marine animals. McGraw-Hill Book Co., New York.
 14. NIESEN, T. M. 2007. Intertidal habitats and marine biogeography of the Oregonian Province, p. 3-17. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 15. OTTAWAY, J. R. 1977. Predators of sea anemones. *Tuatara*. 22:213-221.
 16. PEARSE, V., and L. FRANCIS. 2000. *Anthopleura sola*, a new species, solitary sibling species to the aggregating sea anemone, *A. elegantissima* (Cnidaria: Anthozoa: Actiniaria: Actiniidae). *Proceedings of the Biological Society of Washington*. 113:596-608.
 17. PICKERING. 1846. *Actinaria artemisia*, p. 11. *In: Synopsis of the report on zoophytes of the US Exploring Expedition around the world, under C. Wilkes, USN commander, in the years 1838-1842*. J. D. Dana (ed.). Google eBooks.
 18. RICKETTS, E. F., J. CALVIN, J. W. HEDGEPEETH, and D. W. PHILLIPS. 1985. *Between Pacific tides*. Stanford University Press, Stanford, CA.
 19. SADRO, S. 2001. Cnidaria (Coelenterata), p. 13-23. *In: An identification guide to the larval marine invertebrates of the Pacific Northwest*. A. L. Shanks (ed.). Oregon State University, Corvallis.
 20. SMITH, B. L., and D. C. POTTS. 1987. Clonal and solitary anemones (*Anthopleura*) of western North America: population genetics and systematics. *Marine Biology*. 94:537-546.
 21. WATERS, V. L. 1975. Food preference of the nudibranch *Aeolidia papillosa* and the effect of the defences of the prey on predation. *The Veliger*. 15:174-192.
 22. WEIS, V. M., E. A. VERDE, A. PRIBYL, and J. A. SCHWARZ. 2002. Aspects of the larval biology of the sea anemones *Anthopleura elegantissima* and *A. artemisia*. *Invertebrate Biology*. 121:190-201.

Updated 2015

C.D. Piazzola and T.C. Hiebert

Anthopleura elegantissima

Aggregating or clonal anemone

Phylum: Cnidaria
Class: Anthozoa, Hexacorallia
Order: Actinaria, Nynantheae, Thenaria
Family: Endomyaria, Actiniidae

Taxonomy: *Anthopleura elegantissima* was originally described by Brandt in 1835 as *Actinia elegantissima*. The subclass Zoantharia has been synonymized with Hexacorallia (Hoeksema 2015).

Description

Medusa: No medusa stage in Anthozoans

Polyp:

Size: The average diameter is about 2.5-4 cm, though the maximum is 5 cm (Fautin and Hand 2007). Specimens are often larger in bays than on the open coast (Hand 1955). The illustrated specimen was 3.5 cm high, with a 4.5 cm disc diameter.

Color: The tentacles are tipped with pink, purple or other colors; the illustrated specimen had white, green, and maroon tentacles, and a green disc with maroon radial lines. The column is usually green, and sometimes shades to white at the base (Fautin et al. 1987). The collar is green and acrorhagi are white to yellow (Fautin and Hand 2007) (figs. 2, 3). Puget Sound forms are often pink and green (Ricketts et al. 1985). Some of the green, especially in the tentacles, is caused by symbiotic algae cells (Kozloff 1983); however, the majority of the coloring is from pigment cells produced by the anemone to protect against UV rays. Thus, in darker habitats the greens fade until the anemone is white (Fautin and Hand 2007).

Body: The anemone has a strong collar, broad flat disc, and slender pointed tentacles. The column has longitudinal rows of tubercules, which are adhesive and create a layer of attached shells and debris. Body walls are soft and thin (Haderlie et al. 1980). The column has a groove below the tentacles (fosse) covered by a distinct fold (parapet or collar). The anemone becomes a hemispheric glob when contracted (fig. 3), and blends into its rocky intertidal habitat. It has a hydrostatic skeleton and will emit water when stepped on (Kozloff 1983; Ricketts et al. 1985).

Column: The column can be twice as high as the diameter when extended,

and is hemispherical when contracted. The entire column is covered with round verrucae (tubercules) in longitudinal rows (Hand 1975).

Collar: The parapet is strong, with a well-developed fosse (groove) (fig. 2).

Oral Disc: The oral disc is a large central area without tentacles on the top of the column. It is broad and flat, with radiating lines (mesenterial insertions). It is slightly wider than the column, or of a similar width. The mouth is in the center of the oral disc, and the lips may be swollen or flush with the surface of disc and are not ribbed.

Tentacles: There are more than 24 tentacles (Fautin and Hand 2007). They are pointed, and about 1/4 as long as the diameter of the disc (fig. 3). There is no oral inner ring of tentacles, and usually more than 5 orders (rows) are present. There are no acontia (thread-like defensive structures expelled through column wall).

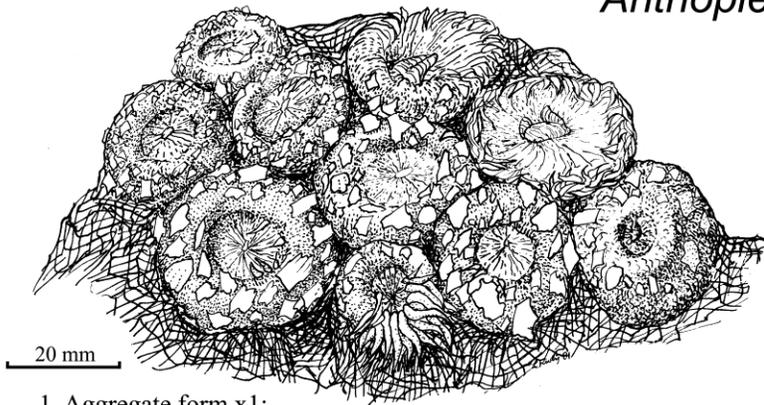
Mesenteries: These are vertical body partitions. There are from 6 in young specimens to more than 24 pairs in mature adults. They are visible at high magnification as vertical lines on column, particularly near the base, and can be irregular, due to asexual fission (not shown).

Pedal Disc: This species has a well-developed pedal disc that attaches to the substrate. Its shape varies from circular to very irregular (Hand 1955). The base is usually the same diameter as column. There are no physa (bulbs) at the base.

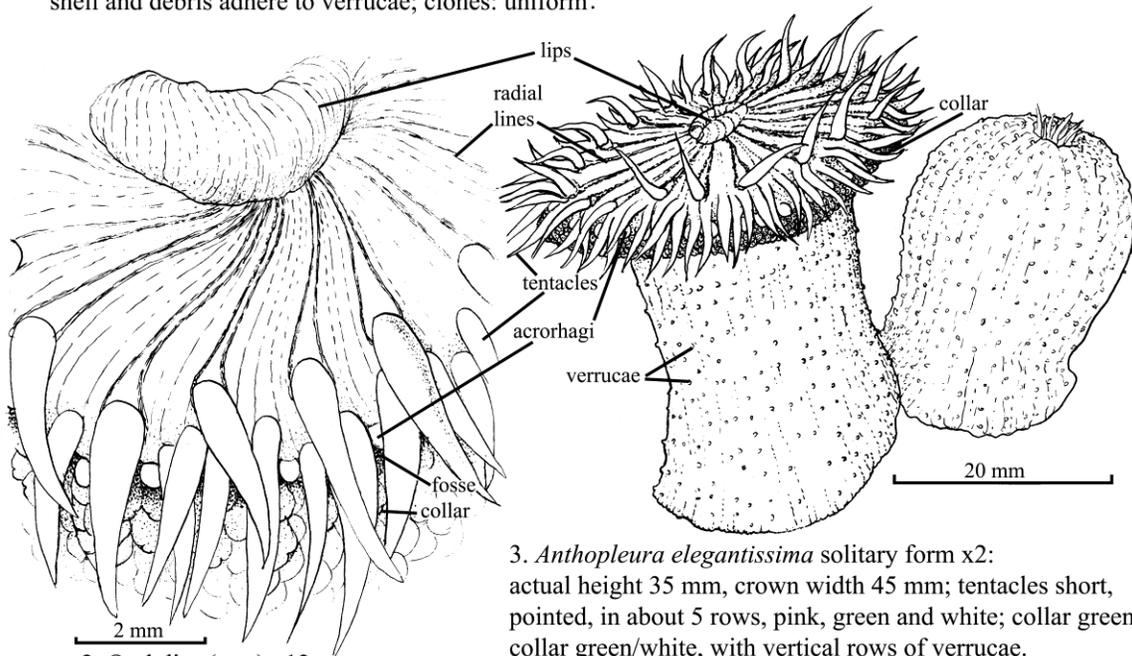
Cnidae: There are several kinds of cnidae in the tentacles, column, acrorhagi, actinopharynx and filaments (not shown); see *Metridium* (Hand 1955).

Acrorhagi: Also known as spherules, these fighting tentacles are round, hollow bodies covered with nematocysts. They are inconspicuous at the top of the column just outside the tentacles (fig. 2) (Hand 1955). tubercules (Fautin and Hand 2007). They are adherent, and collect gravel, shell, and debris. This layer helps prevent desiccation and

Anthopleura elegantissima

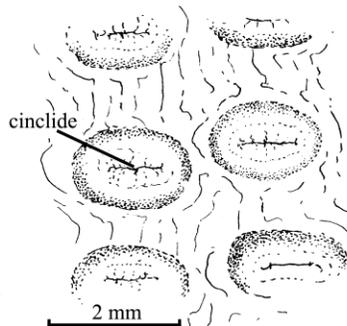


1. Aggregate form x1:
shell and debris adhere to verrucae; clones: uniform.



2. Oral disc (part) x12:
radial lines from mouth to tentacles;
white marginal spherules inside collar.

3. *Anthopleura elegantissima* solitary form x2:
actual height 35 mm, crown width 45 mm; tentacles short,
pointed, in about 5 rows, pink, green and white; collar green;
collar green/white, with vertical rows of verrucae.



4. Verrucae (tubercles) x12.

protects the anemone from UV rays (MacGinitie and MacGinitie 1968; Ricketts et al. 1985). Verrucae on the collar are forked and compound (see *A. artemisia*, fig. 3 in this guide). Those on the column are arranged in distinct longitudinal rows, are not densely packed, and become fewer toward the base ("limbus") (Hand 1955; Fautin and Hand 2007). There are many cinclides (temporary or permanent pores at tips of verrucae) on the column (fig. 4).

Possible Misidentifications

The genus *Anthopleura* can be distinguished from other estuarine anemones (*Metridium*, *Diadumene*) by their acrorhagi inside the fosse under the tentacles, and by the verrucae on their columns. *Anthopleura* always have a well-developed pedal disc and a flat, oral disc with a clear central area. Two other species of *Anthopleura* occur in this area: *Anthopleura xanthogrammica* is a large open coast species occasionally found in the most marine parts of our estuaries. It is very large, solitary (not aggregating), with uniformly colored disc and tentacles (not pink-tipped or with radial lines on the disc). The tentacles are in 5 or more rows (Haderlie et al. 1980). Its verrucae completely cover the column (they are not in rows). *Anthopleura artemisia* has tubercles on the upper 2/3 of its column only; the column is white or pink below and usually gray or black above; tentacles are brightly colored and patterned (red in Coos Bay). *Anthopleura artemisia* is more likely to be found burrowing in a sandy or muddy substrate than *A. elegantissima*, which can live close by. It also lacks the algae symbionts that are found in *A. elegantissima*. A third species of *Anthopleura*, *A. sola*, is very similar in appearance to *A. elegantissima*. The primary difference between the two is that *A. elegantissima* is clonal while *A. sola* is solitary. Though *A. sola* is not found locally, there are many examples in the literature of *A. sola* being misclassified as *A. elegantissima* (Pearse and Francis 2000). Other sand-dwelling anemones might include *Flosmaris grandis*, a southern form, which is vermiform and has a translucent or white column (Fautin and Hand 2007). Most other elongated or tube-dwelling forms, i.e., Order Cerinatharia, are rarely intertidal in our area.

Ecological Information

Range: The type locality is Sitka (Sitchea Islands), Alaska (Brandt 1835). The range is Alaska to southern California.

Local Distribution: In Coos Bay, they can be found in high abundance at Pigeon Point.

Habitat: Specimens are found on rocky substrates in the mid to high intertidal, often in full sun, where it aggregates in beds of up to 20 m and 100,000 animals (Childress 1969; Fautin and Hand 2007). They are especially prevalent in exposed-rocky habitats where sand collects, and are more occasional on open coasts and exposed pilings (Ricketts et al. 1985). When found in sand, *A. elegantissima* is attached to underlying rock, and can be fully buried at times (Fautin and Hand 2007). Algae mats in the intertidal create hospitable, moist habitats for the aggregations (Niesen 2007). Specimens can survive in polluted waters (Ricketts et al. 1985), and can hang from the roof of overhangs (Niesen 2007).

Salinity: Collected at 30.

Temperature: Specimens are kept in lab at 12°C. 20°C is considered high temperature and causes cnidarian bleaching (loss of symbiotic algae) (Richier et al. 2008).

Tidal Level: Found from 0 to +4.5 feet above mean lower low water level (Hand 1955).

Associates: Green algae (zoochlorellae) and dinoflagellates (zooxanthellae) live in the anemone's gut tissue and create some of the green coloring; the algae provide some nutritional value to their host, though the anemone still requires carnivorous meals (Ricketts et al. 1985; Kozloff 1983). The amphipod *Orchomenella recondita* sometimes lives in the digestive cavity. Many organisms, including the amphipods *Gibberosus myersi* and *Macronassa macromera*, the snail *Epitonium tinctum*, and the chiton *Lepidochitona fernaldi*, live in the aggregations (Chapman 2007; McLean 2007; Strathmann and Eernisse 1987).

Abundance: *Anthopleura elegantissima* is the most abundant anemone on the coast (Ricketts et al. 1985), and is the most abundant *Anthopleura* in Coos Bay. The peak of the breeding season is Sept-Oct, and recruitment is late fall-winter (Fautin and Sebens 1987).

Life-History Information

Reproduction: There are both sexual and asexual reproductive cycles. Individual polyps and clonal aggregations are dioecious (Fautin and Sebens 1987). Sexual spawning is in September (San Francisco) (Haderlie et al. 1980). Eggs are freely-spawned and brown, no larger than 250 µm (Sadro 2001), and covered with clusters of spines (Fautin and Sebens 1987). Asexually, anemones divide via longitudinal binary fission, producing aggregations of "clones" common to this species (all are similar in coloration and sex) (Hand 1955; Fautin and Hand 2007). Each division takes about two days to complete, and only the outer edge of the clonal colony divides by fission (MacGinitie and MacGinitie 1968).

Larva: Sexual reproduction produces feeding planula larvae. At three weeks larvae are ovaloid to cylindrical, covered in cilia, and no longer than 250 µm with a 70 µm apical tuft. They actively swim using the cilia on their apical tuft (Sadro 2001; Siebert 1974). They feed by releasing a mucus strand as they swim. The strand collects food particles, and the cilia then pull the strand up to the mouth and ingest it (Siebert 1974). There are no symbiotic algae in the larvae; this relationship between algae and *A. elegantissima* must be established at a later life stage (Siebert 1974).

Juvenile: Anemones are considered juveniles if they are less than 6.5 cm in diameter (Sebens 1982b). They are common in intertidal mussel beds and less common but present in rock crevices. It is possible that they settle higher in the intertidal and migrate lower to the tidepools as they grow (Sebens 1982b).

Longevity: These anemones are reputed to be very long lived, and are especially successful as an aquarium animal (one particular specimen died after about 80 years due to lab failure rather than old age) (Ricketts et al. 1985).

Growth Rate: Specimens reach adult size two years after settlement (Sebens 1982b; Fautin and Sebens 1987). The highest growth rate is concurrent with the lowest clonal division rate in the spring and summer, while the highest division rate and lowest growth rate both occur in the fall and winter (Sebens 1982a).

Food: *Anthopleura elegantissima* is a carnivorous stationary hunter in the tidepools (Niesen 2007) that uses tentacles to capture prey (Ricketts et al. 1985). It primarily eats crustaceans, such as copepods, amphipods, and isopods (Haderlie et al. 1980). Food preference seems to be genetically determined (Waters 1975).

Predators: Specimens are eaten by varied intertidal predators, including seastars. The nudibranchs *Aeolidia papillosa* and *Hermisenda crassicornis* attack the column (McDonald 2007; Ricketts et al. 1985). The snail *Epitonium tinctum* eats the tips of tentacles (McLean 2007).

Behavior: Anemones at the edges of clonal groups will "attack" neighboring clonal aggregations with their acrorhagi, causing wounds; a corridor between clonal groups is thus maintained (Francis 1973; Ricketts et al. 1985). Symbiotic green algae may aid the anemone in modifying phototaxis (Buchsbaum 1968) and in averting starvation (Kozloff 1983). Anemones contract, inflate, and expel nematocysts or detach their pedal disc and move when their column is attacked by the nudibranch *Aeolidia papillosa* (Waters 1975).

Bibliography

1. BRANDT, J. F. 1835. Prodrömus descriptionis animalium ab H. Mertensio in orbis terrarum circumnavigatione observatorum. Google eBooks, Petropoli.
2. BUCHSBAUM, V. M. 1968. Behavioral and physiological responses to light by the sea anemone *Anthopleura elegantissima* as related to its algal symbiotes. PhD. Stanford University.
3. CHAPMAN, J. W., E. L. BOUSFIELD, and D. E. BOWERS. 2007. Amphipoda: Gammaridea, p. 545-618. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. T. Carlton (ed.). University of California Press, Berkeley, CA.
4. CHILDRESS, L. F. 1969. Intra-specific aggression and its relation to the distribution pattern of the clonal sea

- anemone, *Anthopleura elegantissima*. Ph.D. Stanford University.
5. FAUTIN, D. G., and C. HAND. 2007. Anthozoa, p. 173-184. *In: The Light and Smith Manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley.
 6. FAUTIN, D. G., and K. P. SEBENS. 1987. Phylum Cnidaria, Class Anthozoa, p. 83-104. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle.
 7. FAUTIN, D. G., A. E. SIEBERT, and E. N. KOZLOFF. 1987. Class Anthozoa, p. 68-78. *In: Marine invertebrates of the Pacific Northwest*. E. N. Kozloff (ed.). University of Washington Press, Seattle.
 8. FRANCIS, L. 1973. Intraspecific aggression and its effect on the distribution of *Anthopleura elegantissima* and some related sea anemones. *Biological Bulletin*. 144:73-92.
 9. HADERLIE, E. C., C. HAND, and W. B. GLADFELTER. 1980. Cnidaria (Coelenterata): the sea anemones and allies, p. 40-75. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford.
 10. HAND, C. H. 1955. The sea anemones of central California. Part II. The endomyarian and mesomyarian anemones. *Wasmann Journal of Biology*. 13:37-99.
 11. —. 1975. Class Anthozoa, p. 85-93. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
 12. HOEKSEMA, B. 2015. Hexacorallia. Vol. 2015, *World Register of Marine Species*: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=1340>. [Accessed 9/23/2015].
 13. KOZLOFF, E. N. 1983. *Seashore life of the northern Pacific coast*. University of Washington Press, Seattle.
 14. MACGINITIE, G. E., and N. MACGINITIE. 1968. *Natural history of marine animals*. McGraw-Hill Book Co., New York.
 15. MCDONALD, G. R. 2007. Sacoglossa and Nudibranchia, p. 788-807. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 16. MCLEAN, J. H. 2007. Gastropoda, p. 713-739. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 17. NIESEN, T. M. 2007. Intertidal habitats and marine biogeography of the Oregonian Province, p. 3-17. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 18. PEARSE, V., and L. FRANCIS. 2000. *Anthopleura sola*, a new species, solitary sibling species to the aggregating sea anemone, *A. elegantissima* (Cnidaria: Anthozoa: Actiniaria: Actiniidae). *Proceedings of the Biological Society of Washington*. 113:596-608.
 19. RICHIER, S., M. RODRIGUEZ-LANETTY, C. E. SCHNITZLER, and V. M. WEIS. 2008. Response of the symbiotic cnidarian *Anthopleura elegantissima* transcriptome to temperature and UV increase. *Comparative Biochemistry and Physiology D-Genomics & Proteomics*. 3:283-289.
 20. RICKETTS, E. F., J. CALVIN, J. W. HEDGEPEETH, and D. W. PHILLIPS. 1985. *Between Pacific tides*. Stanford University Press, Stanford, CA.
 21. SADRO, S. 2001. Cnidaria (Coelenterata), p. 13-23. *In: An identification guide to the larval marine invertebrates of the Pacific Northwest*. A. L. Shanks (ed.). Oregon State University, Corvallis.

22. SEBENS, K. P. 1982a. Asexual reproduction in *Anthopleura elegantissima* (Anthozoa, Actiniaria): seasonality and spatial extent of clones. *Ecology*. 63:434-444.
23. —. 1982b. Recruitment and habitat selection in the intertidal sea anemones, *Anthopleura elegantissima* (Brandt) and *A. xanthogrammica* (Brandt). *Journal of Experimental Marine Biology and Ecology*. 59:103-124.
24. SIEBERT, A. E. 1974. Description of embryology, larval development, and feeding of sea anemones *Anthopleura elegantissima* and *A. xanthogrammica*. *Canadian Journal of Zoology*. 52:1383-1388.
25. STRATHMANN, M. F., and D. J. EERNISSE. 1987. Phylum Mollusca, Class Polyplacophora, p. 205-219. *In*: *Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle.
26. WATERS, V. L. 1975. Food preference of the nudibranch *Aeolidia papillosa* and the effect of the defenses of the prey on predation. *The Veliger*. 15:174-192.

Updated 2015

C.D. Piazzola and T.C. Hiebert

Diadumene lineata

Orange-striped anemone

Phylum: Cnidaria
Class: Anthozoa, Hexacorallia
Order: Actiniaria, Nynantheae, Thenaria
Family: Acontiaria, Diadumenidae

Taxonomy: *Diadumene lineata* was first described by Verrill in 1869 as *Sagartia lineata*. The subclass Zoantharia has been synonymized with Hexacorallia (Hoeksema 2015). Synonyms include *Haliplanella luciae* (Fautin and Hand 2007).

Description

Medusa: No medusa stage in Anthozoans

Polyp:

Size: A large specimen can be 30 mm high (Kozloff 1983). It is usually not more than 20 mm high and 10 mm diameter (Fautin and Hand 2007)

Color: The color is variable; specimens are usually green with single or double vertical orange, white or yellow stripes (Fautin and Hand 2007), but they can have a brownish or olive column. Gonads are pink or orange and may be visible on the lower column. Mesenteries appear as dark vertical lines. Tentacles are usually colorless, though they can be gray to light green with white flecks (nematocysts) (Hand 1955). The oral disc is transparent and can appear dark because of the dark interior. Lips are dark gray.

Body: This anemone is cylindrical with many fine long tentacles (Fig. 1). Mesenteries divide the internal structure. Defensive tentacles called acontia can extend through pores called cinclides in the column. The parapet rings the end of the column, from which the capitulum extends distally (Fig. 2). On the oral disc, specimens occasionally have ciliated grooves to direct water (siphonoglyphs) and spaces between the mesenteries (endocoels).

Column: The column is a smooth, low cylinder that tapers towards the top and has vertical stripes (often 7-19) (Fautin et al. 1987). Dark mesenteries show through the column. It is dotted with cinclides (portholes through which acontia can protrude) that can be seen by the naked eye.

The column is often scarred by longitudinal fission (asexual reproduction) (Hand 1955).

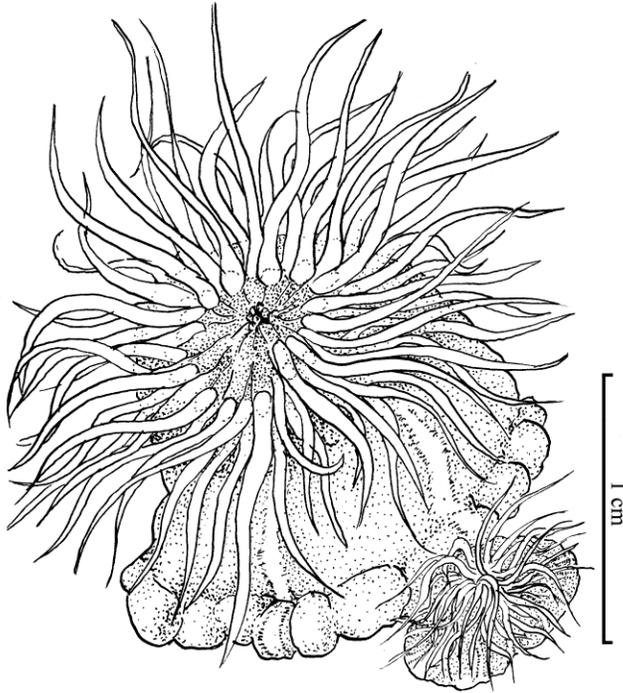
Collar: The collar includes the parapet and capitulum. The capitulum is the top part of the anemone, separated from the column by the parapet (Fig. 2). The capitulum is transparent, usually light green, and without cinclides. There are tentacles around the upper margin of the capitulum. The parapet is noticeable only when anemone is fully extended, and rings the top of the column.

Oral Disc: The mouth is dark and ribbed. The ribs correspond to number of mesenteries. There are 0-3 siphonoglyphs (ciliated grooves on the ends of the mouth that direct water into the pharynx) (none figured). The margin is plain, rather than frilled or lobed (Fautin and Hand 2007). A large area of the disc around the mouth is tentacle-free, with radiating rows of white flecks on the endocoels (spaces between the pairs of mesenteries) (Hand 1955) (Fig. 4).

Tentacles: The number of tentacles is greater than 24 but fewer than 100 (Fautin and Hand 2007). They are retractile and smooth, short and blunt when contracted, and they are not capitate (knobbed). There are only one kind, and there's no oral ring of tentacles. 2 pairs of "directives" (a kind of tentacle close to the ends of mouth) (not figured) are typically present, but this can vary (Hand 1955); when present, these tentacles are marked no differently than the others (Fautin and Hand 2007). They can have up to 18 "catch" tentacles near the mouth, which are short, blunt and opaque (Williams 1975). This species has acontia, which are threadlike defensive structures discharged through the column wall when the anemone is disturbed (Fautin and Hand 2007).

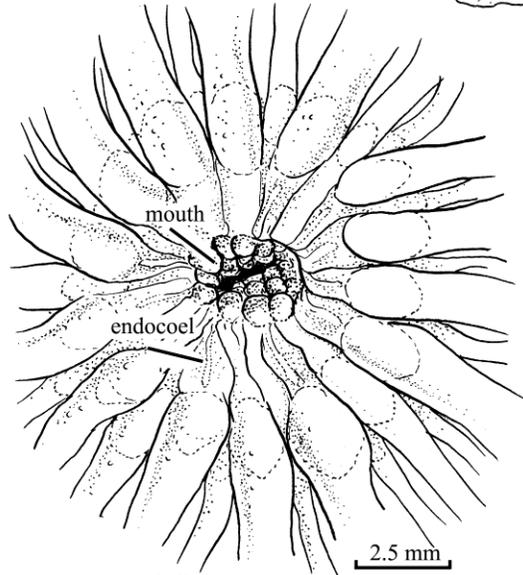
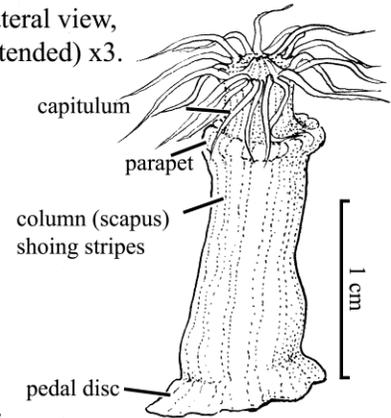
Mesenteries: Mesenteries are vertical internal partitions (usually 6 in this species) visible as dark vertical lines. There are usually more mesenteries distally than near the base

Diadumene lineata

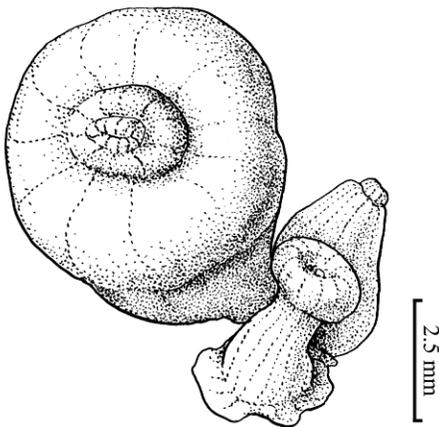


1. *Diadumene lineata* (H:1cm) x4.5:
up to 100 clear, tapered tentacles; low, cylindrical column attached to substrate; oral disc with tentacle-free area; column smooth, green, striped white, yellow or orange; margin not frilled or lobed.

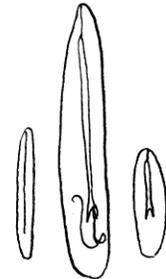
2. Small anemone (lateral view, extended) x3.



4. Oral disc x9:
radiating white endocoels;
large tentacle-free area
dark, ribbed mouth.



3. Contracted anemones x8:
tentacles completely retracted.



5. Nematocysts from acontia x1000 (Hand 1955).

(Hand 1955). Gonads appear as thickened bands on mesentery filaments.

Pedal Disc: At the base, there is a distinct pedal disc, which is circular and attaches to the substrate.

Cnidae: The cnidae are stinging organelles. There are several types present in this species; on the acontia there are 3 kinds (Fig. 5) (Haliplanellidae) (Hand 1955).

Possible Misidentifications

Metridium senile is another anemone found on docks and pilings. However, while *D. lineata* usually has a darker brown or olive-colored column and stripes, *M. senile* has a lighter white or gray column and lacks stripes. *Metridium senile* is also often larger (if only by a centimeter or two) than *D. lineata*.

The anemone most likely to be confused with *Diadumene lineata* is *D. franciscana*, which can be cream to light green with white stripes. It has one pair of directive tentacles (long, retractable tentacles that point toward the mouth), which are yellow at their bases, while *D. lineata*'s are identical to their other tentacles (Fautin and Hand 2007).

Diadumene franciscana usually has 2 siphonoglyphs, pink lips, a rough column, and often an irregular base. Its parapet is poorly developed compared to *D. lineata*'s.

The Puget Sound *Diadumene* is not green but orange, yellowish, grayish, reddish, cream or brown. Other *Diadumene* species are not usually green (Fautin and Hand 2007).

If the specimen is orange striped "it can only be [*D. lineata*]" (Hand 1955).

Ecological Information

Range: The type locality is Hong Kong harbor (Verrill 1869). This anemone is more wide-spread than any other anemone species (Fautin and Hand 2007), and has been found in Europe, North America, and Asia. It was likely introduced to Europe through the Suez Canal in Egypt (Streftaris et al. 2005). In the US Atlantic, it is found on the New England coast, and on the Pacific it is found from the Puget Sound to California. It was likely introduced to the US from Asia with oyster spat (Ricketts et al. 1985).

Local Distribution: It is found in Oregon estuaries. Locally (in Coos Bay), it is found on the Charleston docks and in South Slough.

Habitat: *Diadumene lineata* lives high in the intertidal on rocks and pilings, often in barnacle tests and cracks in wood, in estuarine situations, but they have not been found on the outer coast (Hand 1955; Fautin and Hand 2007). Specimens can tolerate a variety of habitats, from rocks high in the intertidal to eelgrass in mudflats (MacGinitie and MacGinitie 1968; Ricketts et al. 1985). They are often found in fouling communities (Fautin and Hand 2007).

Salinity: This species is euryhaline (Ricketts et al. 1985), and adapts to variations in salinity.

Temperature: *Diadumene lineata* is eurythermal, living in cold and temperate waters (Ricketts et al. 1985; Fautin and Sebens 1987). Contraction and encystment can occur with extreme high temperatures (East Coast) (Williams 1975).

Tidal Level: Shallow waters, high in the intertidal.

Associates: *Metridium* sp. are often found in conjunction with *Diadumene lineata*. They are also found on the mussel *Mytilus edulis* with its accompanying fauna, and they have been reported growing on the stems and roots of the cordgrass *Spartina alterniflora* (Molina et al. 2009).

Abundance: This species is usually found in clonal aggregations (Fautin and Hand 2007). These aggregations can completely cover the surface of logs or pilings. Though stable populations are present year-round, they can have a higher abundance in the summer (Molina et al. 2009).

Life-History Information

Reproduction: This specimen can reproduce both sexually and asexually, the latter by longitudinal fission of the column or pedal laceration (Haderlie et al. 1980). Pedal laceration occurs when the anemone spreads out its base and then tears itself away at the center, leaving parts of the outer base attached to the substrate that can then mature into clonal anemones (MacGinitie and MacGinitie 1968). This process can only occur when the anemone is well-fed and relatively large, and it usually takes many hours (MacGinitie and MacGinitie 1968). Its success is largely due to its ability to colonize quickly (Hausmann 1919; Ricketts et al. 1985). In female specimens, the eggs are

spherical and magenta, while in male specimens the sperm is white (Fukui 1991). During the spawning season in summer, *Diadumene lineata* can be sexed by checking the color of the gametes through the body wall (Fukui 1991). They reproduce through spontaneous broadcast spawning.

Larva: After fertilization, it takes eighteen hours for the embryo to develop into a swimming planula larva (Fukui 1991). These larvae are ciliated and have an apical tuft on their aboral end (Fukui 1991; Sadro 2001).

Juvenile:

Longevity: Unknown

Growth Rate: Unknown

Food: *Diadumene lineata* eats small crustaceans and annelids (Hausmann 1919).

Predators: In San Francisco Bay, the nudibranch *Cuthona perca* eats *Diadumene lineata* (McDonald 2007). Other nudibranchs, like *Hermisenda crassicornis*, also eat this species (McDonald 2007).

Behavior: The catch tentacles are used only for stinging, not feeding, and serve to keep anemones separate (Williams 1975). *Diadumene* is considered one of the faster anemones and, in some studies, has been reported moving three to four inches in an hour (MacGinitie and MacGinitie 1968). It also shows a sensitivity to light in laboratories, and will contract when exposed to bright lights (MacGinitie and MacGinitie 1968).

Bibliography

1. FAUTIN, D. G., and C. HAND. 2007. Anthozoa, p. 173-184. *In: The Light and Smith Manual: intertidal invertebrates from central California to Oregon.* J. T. Carlton (ed.). University of California Press, Berkeley.
2. FAUTIN, D. G., and K. P. SEBENS. 1987. Phylum Cnidaria, Class Anthozoa, p. 83-104. *In: Reproduction and development of marine invertebrates of the northern Pacific coast.* M. F. Strathmann (ed.). University of Washington Press, Seattle.
3. FAUTIN, D. G., A. E. SIEBERT, and E. N. KOZLOFF. 1987. Class Anthozoa, p. 68-78. *In: Marine invertebrates of the Pacific Northwest.* E. N. Kozloff (ed.). University of Washington Press, Seattle.
4. FUKUI, Y. 1991. Embryonic and larval development of the sea anemone *Haliplanella lineata* from Japan. *Hydrobiologia.* 216:137-142.
5. HADERLIE, E. C., C. HAND, and W. B. GLADFELTER. 1980. Cnidaria (Coelenterata): the sea anemones and allies, p. 40-75. *In: Intertidal invertebrates of California.* R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford.
6. HAND, C. 1955. Distribution of *Alderia modesta* in Washington. *Nautilus.* 69:22-28.
7. HAUSMANN, L. A. 1919. The orange-striped anemone (*Sagartia luciae*, Verrill). *Biological Bulletin.* 37:363-371.
8. HOEKSEMA, B. 2015. Hexacorallia. Vol. 2015, *World Register of Marine Species:* <http://www.marinespecies.org/aphia.php?p=taxdetails&id=1340>. [Accessed 9/23/2015].
9. KOZLOFF, E. N. 1983. *Seashore life of the northern Pacific coast.* University of Washington Press, Seattle.
10. MACGINITIE, G. E., and N. MACGINITIE. 1968. *Natural history of marine animals.* McGraw-Hill Book Co., New York.
11. MCDONALD, G. R. 2007. Sacoglossa and Nudibranchia, p. 788-807. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. T. Carlton (ed.). University of California Press, Berkeley, CA.
12. MOLINA, L. M., M. S. VALINAS, P. D. PRATOLONGO, R. ELIAS, and G. M. E. PERILLO. 2009. First record of the sea anemone *Diadumene lineata* (Verrill 1871) associated to *Spartina alterniflora* roots and stems, in marshes at the Bahia Blanca Estuary, Argentina. *Biological Invasions.* 11:409-416.
13. RICKETTS, E. F., J. CALVIN, J. W. HEDGEPEETH, and D. W. PHILLIPS. 1985. *Between Pacific tides.* Stanford University Press, Stanford, CA.
14. SADRO, S. 2001. Cnidaria (Coelenterata), p. 13-23. *In: An identification guide to the larval marine invertebrates of the Pacific Northwest.*

- A. L. Shanks (ed.). Oregon State University, Corvallis.
15. STREFTARIS, N., A. ZENETOS, and E. PAPATHANASSIOU. 2005. Globalisation in marine ecosystems: The story of non-indigenous marine species across European seas. *Oceanography and Marine Biology: An Annual Review*. 43:419-453.
 16. VERRILL, A. E. 1869. Synopsis of the polyps and corals of the North Pacific Exploring Expedition, under Commodore C. Ringgold and Capt. John Rodgers, U.S.N., from 1853-1856. Collected by Dr. Wm. Stimpson, Naturalist to the Expedition.
 17. WILLIAMS, R. B. 1975. Catch tentacles in sea anemones: occurrence in *Haliplanella luciae* (Verrill) and a review of current knowledge. *Journal of Natural History*. 9:241-248.

Updated 2015

C.D. Piazzola and T.C. Hiebert

Nematostella vectensis

Starlet sea anemone

Phylum: Cnidaria

Class: Anthozoa, Hexacorallia

Order: Actiniaria, Nynantheae, Athenaria

Family: Edwardsiidae

Taxonomy: *Nematostella vectensis* was described by Stephenson in 1935.

Nematostella pellucida is a synonym (Hand 1957). In the larger taxonomic scale, the subclass Zoantharia has been synonymized with Hexacorallia (Hoeksema 2015).

Description

Medusa: No medusa stage in Anthozoans

Polyp:

Size: The column (Fig. 1) can be up to 15 mm long in the field, but can grow much longer (160 mm) when raised in the laboratory (Hand and Uhlinger 1992; Fautin and Hand 2007). The maximum diameter is 4 mm at the base near the bulb (physa) (Hand 1957) and increases to 8 mm at the crown of tentacles; the diameter is not often this large, and a more average diameter of the column is 2.5 mm.

Color: The anemone is white and transparent when expanded (Fautin and Hand 2007), while the internal color depends on food.

Body: *Nematostella vectensis* is radially symmetrical, consisting of a tall cylinder and a crown of tentacles. Aberrant forms (e.g., two headed, tentacleless) are found as well (Williams 1976). The body is slightly worm-like, in that the column is longer than it is wide (Fautin et al. 1987). Usually, the anemone is buried up to its oral disc and tentacles (Fautin and Hand 2007). Mesenteries divide the internal structure and cannot be seen through the body walls. On the oral disc, specimens occasionally have ciliated grooves to direct water (siphonoglyphs).

Column: The column is longer than wide, cylindrical, and transparent. The eight mesenteries are visible through its walls. There is a thin capitulum (collar) around the oral disc at the top of the column (Williams 1975). There is a single ventral siphonoglyph (Williams 1975).

Oral Disc: There is no inner ring of tentacles, and there are no siphonoglyphs, on the oral disc.

Tentacles: Tentacles are retractile, cylindrical, and tapered. They are not capitate, or knobbed. Though they can vary from 12-18, there are usually 16 (Stephenson 1935; Fautin and Hand 2007). There are 6-7 outer (exocoelic) tentacles that are longer than inner (endocoelic) tentacles, and are often reflexed down the column (they can be longer than column). The inner tentacles can be raised above the mouth (Fig. 1), and can have white spots on their inner edges (Crowell 1946). Nematosomes can be seen moving inside the tentacles.

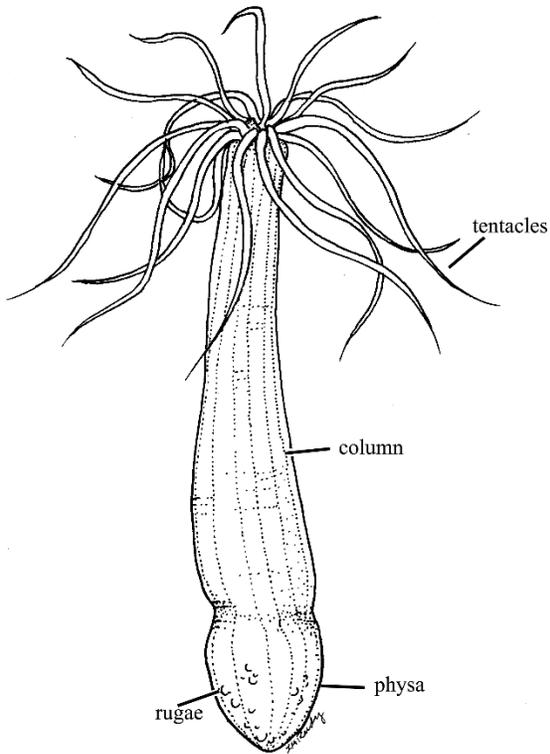
Mesenteries: Mesenteries are vertical partitions (eight in this species) below the gullet and visible through the column. Gonads appear as thickened bands on the mesenteries (Fig. 3) (Lindsay 1975). Eggs are produced from these partitions. The mesenteries can be green, brown, black, etc., depending on food (Williams 1975).

Pedal Disc: The physa is a swollen, bulb-like burrowing structure at the base of the column (Fig. 1), which replaces the pedal disc of other anemones. It is covered with rugae (ridges), which secrete mucus and aid in digging and climbing (Williams 1975). *Nematostella vectensis* does not attach to solid substrate, but rather burrows into muddy habitats (Fautin et al. 1987).

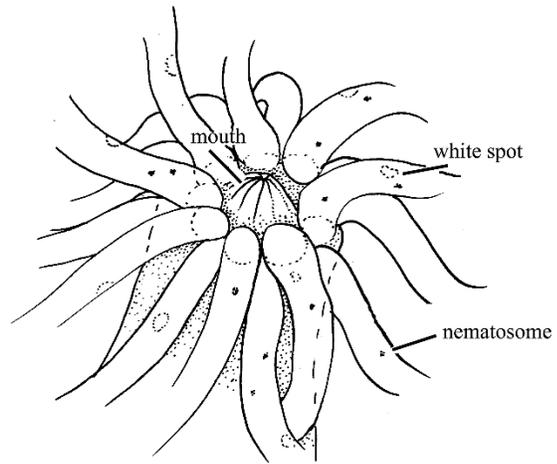
Cnidae: According to Matus et al. (2007), there are three types of cnidae in this species: basitrichs, microbasic basitrichs, and spirocysts.

Nematosomes: These are rather mysterious spherical, ciliated bodies, sometimes found in the coelenteron (digestive cavity) and in tentacles (Fautin et al. 1987) (Fig. 2). They contain nematocysts (Hand and Uhlinger 1992), and their function is not known.

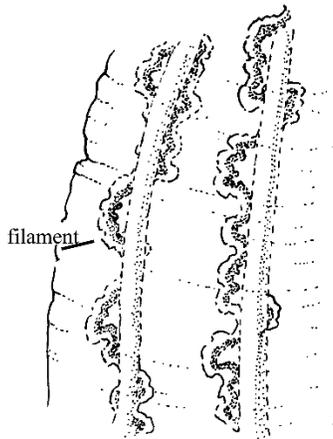
Nematostella vectensis



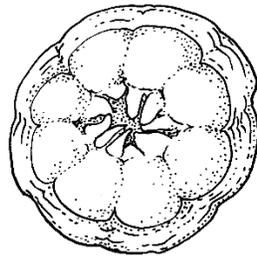
1. *Nematostella vectensis* x10:
cylindrical column; physa with rugae;
12-18 transparent tentacles, white spotted;
actual size 11 mm.



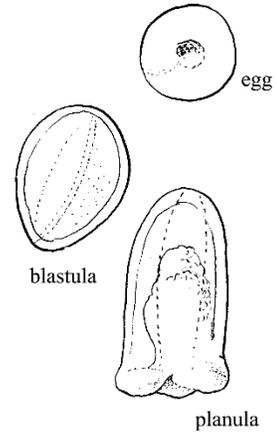
2. Crown of tentacles x30:
usually 16 white-spotted tentacles; nematosomes visible;
mouth cone-shaped.



3. Menenteries (seen through
column wall) x30: 8 vertical
partitions; filaments contain eggs .



4. Dorsal view,
tentacles retracted x40.



5. Development.

Possible Misidentifications

This is the only species of the genus *Nematostella* known in the temperate northern hemisphere. *Nematostella polaris*, a similar Arctic anemone, lives under conditions which *N. vectensis* could tolerate. They are not believed to be the same species (Hand 1957). There is certainly no other very small, mud-dwelling burrowing anemone in our area, which could be confused with *N. vectensis*. *Flosmaris grandis* is another elongate, mud-burrowing, translucent anemone, but it is usually very large (to 50 cm), has over 24 tentacles, and instead of a physa, has a basal disc attached to something solid (Fautin and Hand 2007). This species also has acontia (defensive tentacles that extrude through the column), which *N. vectensis* lacks (Fautin and Hand 2007). *Diadumene* sp. are often long and pale, but they have pigmentation of some sort and don't burrow. Only *N. vectensis* of these anemones has nematosomes.

Ecological Information

Range: The type locality is the Isle of Wight, where it likely no longer exists due to destruction of habitat (Williams 1975). Its range covers the Atlantic coasts of Europe; from Florida to Louisiana in the Gulf of Mexico; the east coast of North America from Nova Scotia to Georgia; and the west coast of North America from California to Washington (Hand and Uhlinger 1992; Fautin and Hand 2007).

Local Distribution: Locally, *N. vectensis* is found at five sites in Coos Bay, including in South Slough, near downtown Coos Bay, and at the mouth of Coos River.

Habitat: This species is primarily estuarine (in temperate northern estuaries), and is common in shallow pools of salt marshes (Fautin et al. 1987; Fautin and Hand 2007). It often lives in pondweed masses, like soft muds of *Salicornia* marshes; *Ruppia*, *Cladophora*, and *Chaetomorpha* ponds (New England); and *Enteromorpha* and *Vaucheria* ponds (Coos Bay) (Williams 1976). These anemones are sensitive to pollution, and so will not be found in habitats that become contaminated (Williams 1976).

Salinity: *Nematostella vectensis* can tolerate a wide range of salinities, from less than 50‰ seawater to over 100‰ in Coos Bay (Hand 1957). It is an osmoconformer, has been

found from 8 to 38, and is very adaptable to salinity changes (Inouye 1976).

Temperature: This species lives in a wide range of temperatures; in northern California alone, it can be found from 0-30° C (Hand 1957). It has been kept for long periods in the lab at 21-22° C (Inouye 1976). In Coos Bay (South Slough), it ranges from 6-18° C (ibid).

Tidal Level: This anemone is generally found in salt marsh tide pools above + 3 ft, but is sometimes found living subtidal (Hand and Uhlinger 1992).

Associates: It often lives in association with the algae *Distichlis*, *Salicornia*, and *Enteromorpha*; the diatom *Vaucheria*; and the invertebrates nemerteans, polychaete larvae, harpacticoid copepods, ciliates, sphaeromid isopods, and gammarid amphipods.

Abundance: A rarely occurring animal, it can be densely abundant over a small area where it does occur (Hand and Uhlinger 1992). Because of its sensitivity to pollution, it quickly retreats from areas where the habitat is compromised.

Life-History Information

Reproduction: This anemone propagates using both sexual and asexual reproduction. It is dioecious (separate sexes) (Hand and Uhlinger 1992), and its gonads on the mesenteries produce gametes. Animals are found with developed gonads in summer and fall (Williams 1976), but in laboratory settings they will reproduce year-round (Hand and Uhlinger 1992). Egg production can be induced in lab by lowering salinity (Lindsay 1975); the eggs are released in sticky, gelatinous egg masses that also contain nematosomes (Hand and Uhlinger 1992). In lab these anemones can maintain a schedule of spawning once a week (Hand and Uhlinger 1992). Sexual reproduction produces planula larvae, which settle as new polyps. There is no medusoid stage. It takes two to three days for the fertilized egg to grow to a planula, and seven days to setting into a juvenile (Hand and Uhlinger 1992). Asexual reproduction is also possible by transverse binary fission (Fautin and Hand 2007). This division can occur in two ways. In the first (physal pinching), the column constricts until a piece of the physa is divided from the rest of the body. This piece develops into a full clonal anemone. In the second, less common way

(polarity reversal), the aboral end of the anemone develops into an oral structure, and the anemone pinches off in the middle to yield two fully-formed anemones (Darling et al. 2005).

Larva: Spherical ciliated planula larvae develop 2 days after fertilization (Hand and Uhlinger 1992). They will change shape as they develop to become elongate and have an apical tuft (Hand and Uhlinger 1992). They actively swim using the cilia on their apical tuft (Sadro 2001).

Juvenile: When it settles, the juvenile has four tentacles and is 250-500 µm long (Hand and Uhlinger 1992). This process occurs about a week after fertilization. Two to three weeks after fertilization it grows more tentacles and has formed all eight mesenteries (Hand and Uhlinger 1992).

Longevity: Specimens have been kept in lab for up to five years (Hand and Uhlinger 1992).

Growth Rate: This species can grow from fertilization to sexual maturity in 69 days, though the process usually takes three to four months (Hand and Uhlinger 1992).

Food: Like other anemones, *N. vectensis* is an active predator, using tentacles with stinging nematocysts to capture prey. Its diet largely consists of the snail *Hydrobia* (New England, Nova Scotia) (Frank 1978), copepods, midge larvae, egg masses, crustacean remains, ostracods, varied worms, corixids, rotifers, and veliger larvae (Hand and Uhlinger 1994). It is unique in that it also eats insects (Hand and Uhlinger 1994). In lab, it can be fed *Artemia* nauplii, bivalve veliger larvae, mussel tissue, and yolk from hard-boiled hen eggs (Hand and Uhlinger 1992).

Predators: This species is an important prey item for the grass shrimp *Palaemonetes pugio* (Kneib 1985). As of 2008, this shrimp was the only known predator of *N. vectensis* (Moran et al. 2008).

Behavior: Specimens are usually buried to the tentacles, but they are also found extended over the mud. The anemone can move by short, peristaltic-like movements, or by throwing itself (Lindsay 1975). It secretes a mucus "tube" to protect its epidermis (Crowell 1946). This species has also become an important specimen in genetic research due to its short generation time and tolerance to most conditions, among other reasons (Hand and Uhlinger 1992; Darling et al. 2005), and

its genome has been mapped (Putnam et al. 2007).

Bibliography

1. CROWELL, S. 1946. A new sea anemone from Woods Hole, Massachusetts. *Journal of the Washington Academy of Sciences*. 36:57-60.
2. DARLING, J. A., A. R. REITZEL, P. M. BURTON, M. E. MAZZA, J. F. RYAN, J. C. SULLIVAN, and J. R. FINNERTY. 2005. Rising starlet: the starlet sea anemone, *Nematostella vectensis*. *Bioessays*. 27:211-221.
3. FAUTIN, D. G., and C. HAND. 2007. Anthozoa, p. 173-184. *In: The Light and Smith Manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley.
4. FAUTIN, D. G., A. E. SIEBERT, and E. N. KOZLOFF. 1987. Class Anthozoa, p. 68-78. *In: Marine invertebrates of the Pacific Northwest*. E. N. Kozloff (ed.). University of Washington Press, Seattle.
5. FRANK, P. G., and J. S. BLEAKNEY. 1978. Asexual reproduction, diet and anomalies of the anemone *Nematostella vectensis* in Nova Scotia. *Canadian Field-Naturalist*. 92:259-263.
6. HAND, C. 1957. Another sea anemone from California and the types of certain California anemones. *Journal of the Washington Academy of Sciences*. 47:411-414.
7. HAND, C., and K. R. UHLINGER. 1992. The culture, sexual and asexual reproduction, and growth of the sea anemone *Nematostella vectensis*. *Biological Bulletin*. 182:169-176.
8. —. 1994. The unique, widely distributed, estuarine sea anemone, *Nematostella vectensis* Stephenson: A review, new facts, and questions. *Estuaries*. 17:501-508.
9. HOEKSEMA, B. 2015. Hexacorallia. Vol. 2015, *World Register of Marine Species*: <http://www.marinespecies.org/aphia.p>

- hp?p=taxdetails&id=1340. [Accessed 9/23/2015].
10. INOUE, S. 1976. Tolerance of salinity fluctuation by the estuarine sea anemone, *Nematostella vectensis*. Vol. Summer Book 1, Oregon Institute of Marine Biology, Charleston, OR.
 11. KNEIB, R. T. 1985. Predation and disturbance by grass shrimp, *Palaemonetes pugio* Holthuis, in soft-substratum benthic invertebrate assemblages. *Journal of Experimental Marine Biology and Ecology*. 93:91-102.
 12. LINDSAY, J. A. 1975. A salt marsh anemone. *Marine Aquarist*. 6:43-48.
 13. MATUS, D. Q., K. PANG, M. DALY, and M. Q. MARTINDALE. 2007. Expression of Pax gene family members in the anthozoan cnidarian, *Nematostella vectensis*. *Evolution & Development*. 9:25-38.
 14. MORAN, Y., H. WEINBERGER, A. M. REITZEL, J. C. SULLIVAN, R. KAHN, D. GORDON, J. R. FINNERTY, and M. GUREVITZ. 2008. Intron retention as a posttranscriptional regulatory mechanism of neurotoxin expression at early life stages of the starlet anemone *Nematostella vectensis*. *Journal of Molecular Biology*. 380:437-443.
 15. PUTNAM, N. H., M. SRIVASTAVA, U. HELLSTEN, B. DIRKS, J. CHAPMAN, A. SALAMOV, A. TERRY, H. SHAPIRO, E. LINDQUIST, V. V. KAPITONOV, J. JURKA, G. GENIKHOVICH, I. V. GRIGORIEV, S. M. LUCAS, R. E. STEELE, J. R. FINNERTY, U. TECHNAN, M. Q. MARTINDALE, and D. S. ROKHSAR. 2007. Sea anemone genome reveals ancestral eumetazoan gene repertoire and genomic organization. *Science*. 317:86-94.
 16. SADRO, S. 2001. Cnidaria (Coelenterata), p. 13-23. *In: An identification guide to the larval marine invertebrates of the Pacific Northwest*. A. L. Shanks (ed.). Oregon State University, Corvallis.
 17. STEPHENSON, T. A. 1935. *The British sea anemones*. The Ray Society, London.
 18. WILLIAMS, R. B. 1975. A redescription of the brackish-water sea anemone *Nematostella vectensis* Stephenson, with an appraisal of congeneric species. *Journal of Natural History*. 9:51-64.
 19. —. 1976. Conservation of the sea anemone *Nematostella vectensis* in Norfolk, England, and its world distribution. *Transactions of the Norfolk and Norwich Naturalists' Society*. 23:257-266.

Updated 2015

C.D. Piazzola and T.C. Hiebert

Metridium senile

Plumose or frilled anemone

Phylum: Cnidaria
Class: Anthozoa, Hexacorallina
Order: Actinaria
Family: Metridiidae

Taxonomy:

Metridium senile was first described by Linnaeus in 1761. When it was first described, scientists believed that there was only one, very diverse species of *Metridium*: *M. senile*. Hand (1955) took the first step in dividing this species by distinguishing the Atlantic and Pacific populations as subspecies. Since then, further work has been done to determine the genetic lines that should be drawn in *Metridium* sea anemones. Bucklin and Hedgecock (1982) determined that the clonal *M. senile*, the solitary *M. senile*, and the recently (at the time) described *M. exilis* were genetically distinct species. The clonal species kept the name *M. senile*, while the solitary species gained the name *M. gigantus*, which then became *M. farcimen* (Fautin and Hand 2000). There is still some debate on the matter. Recent studies are suggesting that the Atlantic subspecies of *M. senile* may actually be *M. dianthus*, but further research is necessary to fully understand this relationship (Fautin and Sebens 1987; Fautin 2013; Fautin 2015). In the larger taxonomic scale, the subclass Zoantharia has been synonymized with Hexacorallia (Hoeksema 2015).

Description

Medusa: No medusa stage in Anthozoans

Polyp:

Size: Specimens average about 5 cm (2 inches) in diameter, including tentacles. Maximum height is 10 cm, while average is 5 cm (Fautin et al. 1987) and minimum is usually larger than 2 cm (Fautin et al. 1987).

Color: Juveniles are white. Adults can be brown, orange, white, or grey, and cinclides (pores through which acontia can protrude) are sometimes visible as dark spots (Fautin et al. 1987). The tentacles are grey to white, and there is usually a ring of white around the mouth (Kozloff 1983). Because of asexual reproduction, all animals in one area may be same color.

Body: This anemone is cylindrical with many fine short tentacles. Mesenteries divide the internal structure and cannot be seen through the body walls. Defensive tentacles called acontia can extend through pores called cinclides in the column. The parapet rings the end of the column, from which the capitulum extends distally. On the oral disc, specimens occasionally have ciliated grooves to direct water (siphonoglyphs).

Column: The column is stout. It is compact in young specimens and often long in old ones. It is not striped (Perkins 1977).

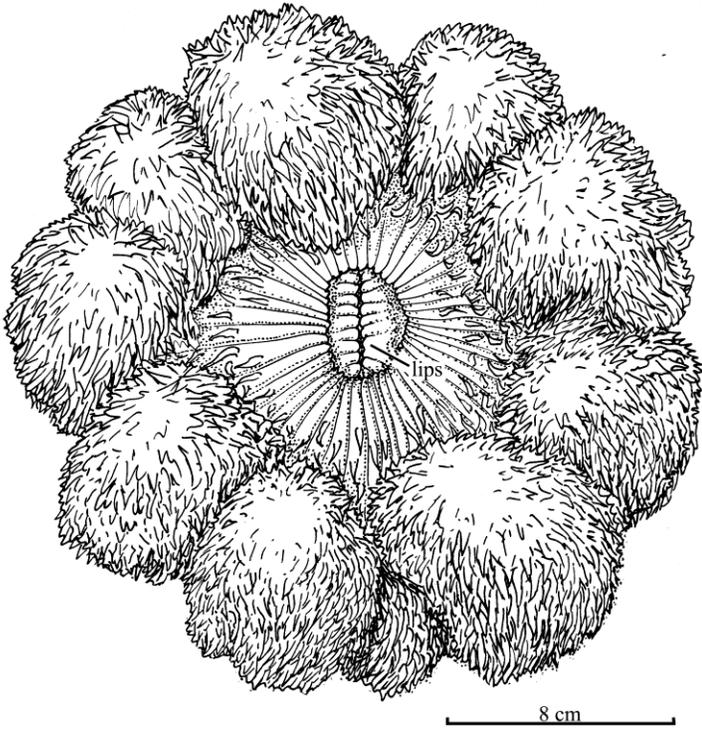
Collar: A parapet (collar) is seen beneath the crown of tentacles (Fig. 2).

Oral Disc: There is very little tentacle-free area around mouth (Fautin and Hand 2007). Siphonoglyphs (ciliated grooves) vary from 0-3, and one is usual (Hand 1955). It is sometimes very slightly lobed, and sometimes it is not lobed at all (Fautin et al. 1987; Fautin and Hand 2007). The margin is frilled (Fautin and Hand 2007).

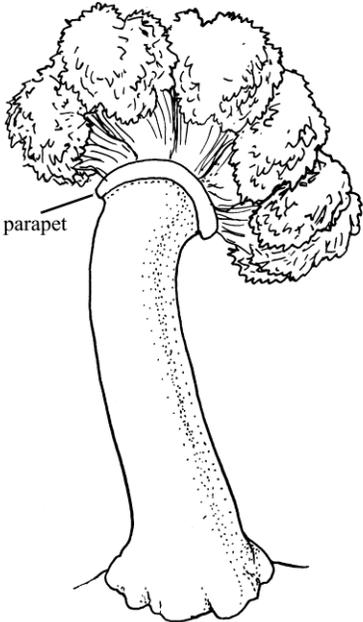
Tentacles: Tentacles are fine, unknobbed, and short. *Metridium senile* can have up to 18 "catch" tentacles; these are short, blunt and opaque near the mouth (Haderlie et al. 1980) and are used to attack anemones from another clonal group or of another species (Ricketts et al. 1985). There are varied accounts of the maximum number of tentacles, but some say that this anemone cannot have more than 100 (Fautin et al. 1987). Tentacles arranged in lappet-like groups or lobes (Fig. 1). Acontia are threadlike tentacles that are found in the lower part of mesenteries. They are discharged through the lower column wall when the animal is disturbed (Fautin et al. 1987).

Mesenteries: These are vertical body cavity partitions. There can be 3-15 pairs in this anemone, but they are not visible through the body wall, as the animal is opaque.

Metridium senile

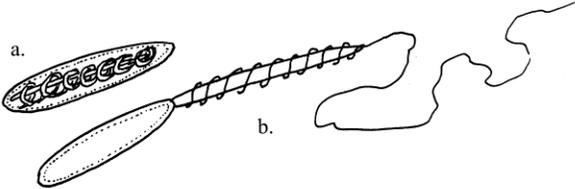


1. *Metridium senile* (dorsal view, D: 24cm): large subtidal specimen, many small tentacles in lobe-like groups; column stout, not striped; base flat, attached; oral disc with obvious lips.



2. Subtidal specimen (lateral view) x1.

3. Nematocysts (generalized):
 a. undischarged.
 b. discharged.



4. Small piling specimen (D: 6cm) x1.

Pedal Disc: This is flat and attached to a hard surface.

Cnidae: There are several kinds of cnidae present (Hand 1955), especially in specimens with catch tentacles (Ricketts et al. 1985); (Fig. 3a, b). Some contain a toxin with a protein fraction that dialyzable material with aromatic amines.

Possible Misidentifications

Anthopleura artemesia, an estuarine anemone with a white stalk, can be confused with young *M. senile*. *Anthopleura artemesia* lives in fine sand, not on pilings, and when extended tentacles are either pink or green and are heavy.

There are two other species of *Metridium* locally:

Metridium exilis lives under rocks and other ledges on the open coast. It has fewer than 100 tentacles with more area around the mouth clear of tentacles, while *M. senile* has very little area on the oral disc without tentacles. *Metridium exilis* has a yellow, orange or red column rather than white, brown, or grey (Fautin and Hand 2007). *Metridium farcimen* was once considered conspecific with *M. senile*. Where *M. senile* is smaller, intertidal, and clonal, *M. farcimen* is large (up to a meter in height), subtidal, and solitary (Fautin and Hand 2000; Eash-Loucks and Fautin 2012). *M. farcimen* also has a highly lobed oral disc, while the oral disc of *M. senile* is simply circular (Fautin and Hand 2007). Finally, the two species have different kinds of cnidae on their acontia (Fautin and Hand 2000). Many older descriptions of *M. senile* are actually of *M. farcimen*.

Ecological Information

Range: The type locality is San Francisco Bay (Hand 1955). This species is circumpolar in the northern hemisphere. They are found in harbors and bays in both the Atlantic and Pacific Oceans. On the Pacific Coast, they can be found from Sitka, Alaska, to Santa Barbara, California.

Local Distribution: Locally, *M. senile* is found on protected pilings in larger Oregon estuaries, such as Coos Bay.

Habitat: This anemone likes bare, shaded pilings and rock jetties, as well as floats in harbors or bays. It can also attach to dead shells, the tunicate *Styela*, the kelp crab

Pugettia, and barnacle tests (Ricketts et al. 1985).

Salinity: Collected at 30 in Coos Bay and at 27 in Puget Sound (communication, R. Boomer). Because this anemone lives in estuaries, it can tolerate brackish conditions; it can survive in salinities of ~15 (50% sea water) (Shumway 1978).

Temperature: This species is found in temperate to cold waters (Hand 1955). Its metabolic rate is often positively correlated with temperature, and it acclimates well.

Tidal Level: This anemone is primarily intertidal. It can tolerate limited exposure, and is found between 0.0 and -1.0 on some pilings, especially in summer (Kozloff 1983). It is most abundant at slightly above mean low low water intertidal (Fautin et al. 1987; Fautin and Hand 2007).

Associates: In Puget Sound, *M. senile* is often found in conjunction with *Diadumene lineata*. On protected pilings, it frequently lives with the sea star *Pisaster* and the tunicates *Styela* and *Cnemidocarpa* (Ricketts et al. 1985). Both juveniles and adults of the sea spider *Pycnogonum litorale* parasitize *M. senile* by sticking their proboscis through the anemone's body wall and ingesting their body fluids (Wilhelm et al. 1997).

Abundance: *Metridium senile* is often found on pilings, floats, and jetties of both Pacific and Atlantic bays and harbors. It is especially abundant in dark quiet corners, and tends to live in clonal clusters (Fautin and Hand 2007).

Life-History Information

Reproduction: Like other anemones, this species reproduces both sexually and asexually. Sexually, *M. senile* is oviparous and dioecious (has separate sexes). It discharges eggs or sperm from its mouth into the water in broadcast spawning (Kozloff 1983). Sperm is released first, and its presence triggers the females to release their eggs (Ricketts et al. 1985). For most specimens, sexual reproduction occurs annually (Hoffmann 1987). Sperm have wedge shaped heads, while eggs are pinkish and about 0.1 mm diameter. The sperm and eggs fertilize to create a planular larva, which settles as a young anemone. Asexually, these anemones can reproduce through pedal laceration and, less commonly, through longitudinal fission (Kozloff 1983). In pedal

laceration, a small amount of the pedal disc is left on substrate as anemone moves about; each small clump forms a new anemone (Fautin and Hand 2007). Asexual reproduction accounts for the often irregular siphonoglyphs and mesenteries, which make *M. senile* a poor choice for lab use (Hyman 1940). Peak of the breeding season is August to September (Fautin and Sebens 1987)

Larva: This species produces pelagic feeding planula larvae (Fautin and Sebens 1987). They are ovaloid to cylindrical, covered in cilia, and have an apical tuft. They actively swim using the cilia on their apical tuft (Sadro 2001).

Juvenile: Juveniles from sexual reproduction are recruited annually (Hoffmann 1987). However, this larval recruitment is less common than juveniles created through asexual reproduction; it is possible that predator *Aeolidia papillosa* is responsible for limiting the survival of small, young anemones (Hoffmann 1987).

Longevity: This species survives well in small aquaria with running seawater.

Growth Rate: The time from pedal laceration to a complete (about small) anemone is about three weeks (Fautin et al. 1987).

Food: *Metridium senile* is an active predator and carnivore. It eats very small organisms, unlike many anemones which manage larger prey (Kozloff 1983). Also eats algae *Enteromorpha intestinalis* and *Desmarestia viridis* (Perkins 1977). Copepods and other varied larvae, without preferential selection (Ricketts et al. 1985).

Predators: This species is popular food for nudibranchs like *Hermisenda crassicornis*, *Aeolidiella chromosoma*, *Aeolidiella oliviae* (McDonald 2007), and *Aeolidia papillosa* (MacGinitie and MacGinitie 1968; Ricketts et al. 1985).

Behavior: In dense groups of small animals, catch tentacles, used for stinging rather than feeding, serve to keep anemones separate (Haderlie et al. 1980). At low tide they can be seen on the sides of pilings hanging "fully relaxed and pendulous" (Ricketts et al. 1985).

Bibliography

- BUCKLIN, A., and D. HEDGECOCK. 1982. Biochemical genetic evidence for a 3rd species of *Metridium* (Coelenterata, Actiniaria). *Marine Biology*. 66:1-7.
- EASH-LOUCKS, W. E., and D. G. FAUTIN. 2012. Taxonomy and distribution of sea anemones (Cnidaria: Actiniaria and Corallimorpharia) from deep water of the northeastern Pacific. *Zootaxa*:1-80.
- FAUTIN, D. G. 2013. Hexacorallians of the World, <http://geportal.kgs.ku.edu/hexacoral/anemone2/index.cfm>. [Accessed 10/22/2015].
- . 2015. *Metridium senile* (Linnaeus, 1761). *In: Hexacorallians of the World*. D. G. Fautin (ed.), *World Register of Marine Species*: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=100982>. [Accessed 10/22/2015].
- FAUTIN, D. G., and C. HAND. 2000. *Metridium farcimen*, the valid name of a common north Pacific sea anemone (Cnidaria: Actiniaria: Acontaria). *Proceedings of the Biological Society of Washington*. 113:1151-1161.
- . 2007. Anthozoa, p. 173-184. *In: The Light and Smith Manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley.
- FAUTIN, D. G., and K. P. SEBENS. 1987. Phylum Cnidaria, Class Anthozoa, p. 83-104. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle.
- FAUTIN, D. G., A. E. SIEBERT, and E. N. KOZLOFF. 1987. Class Anthozoa, p. 68-78. *In: Marine invertebrates of the Pacific Northwest*. E. N. Kozloff (ed.). University of Washington Press, Seattle.
- HADERLIE, E. C., C. HAND, and W. B. GLADFELTER. 1980. Cnidaria (Coelenterata): the sea anemones and allies, p. 40-75. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C.
- BUCKLIN, A., and D. HEDGECOCK. 1982. Biochemical genetic evidence

- Haderlie (eds.). Stanford University Press, Stanford.
10. HAND, C. 1955. The sea anemones of Central California. Part III. The Acontiarian anemones. *Wasmann Journal of Biology*. 13:190-206.
 11. HOEKSEMA, B. 2015. Hexacorallia. Vol. 2015, *World Register of Marine Species*:
<http://www.marinespecies.org/aphia.php?p=taxdetails&id=1340>. [Accessed 9/23/2015].
 12. HOFFMANN, R. J. 1987. Short-term stability of genetic structure in populations of the sea anemone *Metridium senile*. *Marine Biology*. 93:499-507.
 13. HYMAN, L. H. 1940. *The Invertebrates: Protozoa through Ctenophora*. McGraw-Hill, New York, London.
 14. KOZLOFF, E. N. 1983. *Seashore life of the northern Pacific coast*. University of Washington Press, Seattle.
 15. MACGINITIE, G. E., and N. MACGINITIE. 1968. *Natural history of marine animals*. McGraw-Hill Book Co., New York.
 16. MCDONALD, G. R. 2007. Sacoglossa and Nudibranchia, p. 788-807. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 17. PERKINS, E. G. 1977. *Metridium senile*: a clonal formation analysis. Vol. Summer: Book 4. Oregon Institute of Marine Biology (University of Oregon), Charleston, OR.
 18. RICKETTS, E. F., J. CALVIN, J. W. HEDGEPEETH, and D. W. PHILLIPS. 1985. *Between Pacific tides*. Stanford University Press, Stanford, CA.
 19. SADRO, S. 2001. Cnidaria (Coelenterata), p. 13-23. *In: An identification guide to the larval marine invertebrates of the Pacific Northwest*. A. L. Shanks (ed.). Oregon State University, Corvallis.
 20. SHUMWAY, S. E. 1978. Activity and respiration in anemone, *Metridium senile* (L) exposed to salinity fluctuations. *Journal of Experimental Marine Biology and Ecology*. 33:85-92.
 21. WILHELM, E., D. BUCKMANN, and K. H. TOMASCHKO. 1997. Life cycle and population dynamics of *Pycnogonum littorale* (Pycnogonida) in a natural habitat. *Marine Biology*. 129:601-606.

Updated 2015

C.D. Piazzola and T.C. Hiebert

Nemertea

Carinoma mutabilis

A ribbon worm

Phylum: Nemertea
Class: Anopla
Order: Paleonemertea
Family: Carinomidae

Taxonomy: Originally described as *Carinoma griffini* by Griffin (1898), this species was re-described by Coe (1904) as *Carinoma mutabilis*. Initially, two varieties were described (*C. mutabilis argillina* and *C. mutabilis vasculosa*) based on size and degree of muscle development but these differences were determined to be intraspecific variation (Gibson 1995).

Description

Size: Great size variation is reported for this species, from 2.5 to 50 cm, although few are over 20 cm on the California coast. The largest width is 3–5 mm with average sizes much less (Coe 1901, 1905; Kozloff 1974). Specimens are approximately 14 cm in length and 1 mm in width when preserved (Griffin 1898).

Color: Homogeneous (no variation dorso-ventrally). Anterior and head milk white, not translucent, sometimes with brownish mottling (Coe 1901). Intestinal region cream or brownish where internal organs show as transverse dark lines. Males dark yellow or orange, females reddish (Griffin 1898; Kozloff 1974) (Fig. 1). Posterior-most region white (Griffin 1898).

General Morphology: Soft, elongate (but not stretchy) non-segmented (phylum Nemertea).

Body: Thickened and rounded anteriorly, slightly compressed dorso-ventrally from behind head and very flattened posteriorly (Fig. 1). Individuals tend to coil from the sides posteriorly (Coe 1905).

Anterior: Anterior shape changes constantly and can be rounded or elongate. Head is wider than neck and not distinctly marked from the body (Coe 1901). When crawling, head is narrower than body with slight narrowing at neck (Griffin 1898). No cephalic grooves (order Paleonemertea).

Trunk:

Posterior: No caudal cirrus.

Eyes/Eyespots: No ocelli.

Mouth: Just behind brain (class Anopla).

Proboscis: Eversible (phylum Nemertea) and, when not everted, coiled inside rhynchocoel (cavity). No stylets and proboscis pore (opening to rhynchocoel) almost terminal.

Tube/Burrow: Individuals are commonly surrounded by thin sandy mucous tube and worms are happiest in the lab if allowed to burrow in sand.

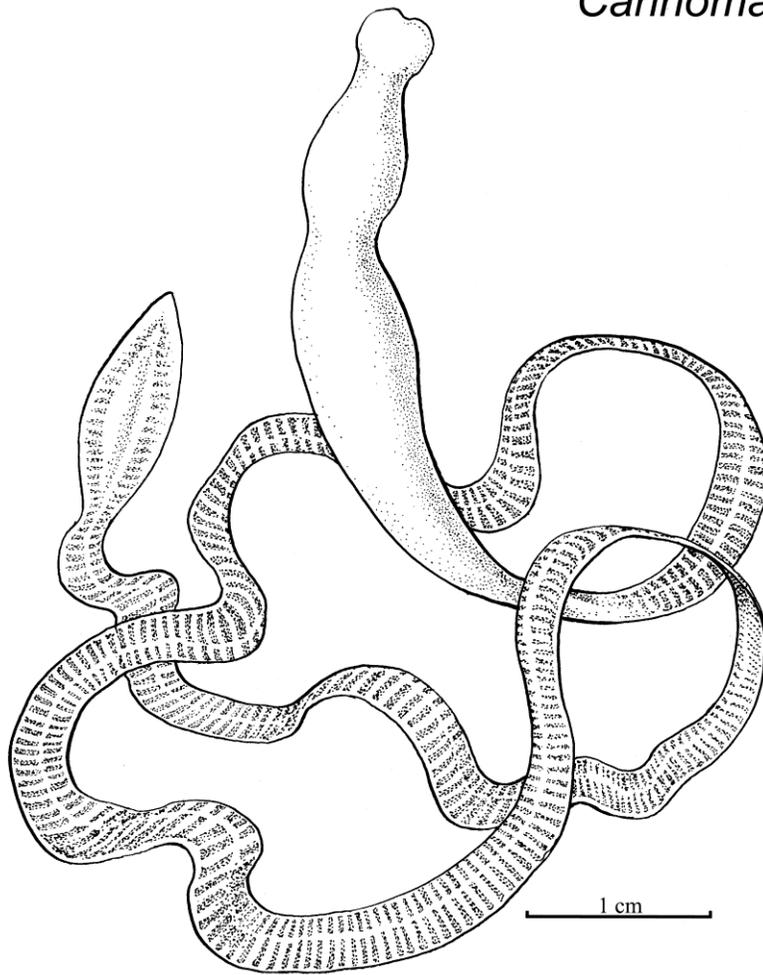
Possible Misidentifications

The Genus *Carinoma* is small and comprises seven described species worldwide including (Gibson 1995): *C. patagonia*, intertidal from southern Chile (Magellan Straits); *C. patriciae*, an Australian species found in silty sand, mud and shell mix; *C. tremaphoros*, intertidal and sublittoral in sand and mud from the Atlantic and Gulf coasts; *C. hamanako* occurs in sand and mudflats near Honshu, Japan (Kajihara et al. 2011); *C. armandi* occurs in the low intertidal and is found among polychaete tubes in the British Isles; *C. crabica* from the Venezuelan coast in Curaçao (Gibson 1995).

C. mutabilis is believed to be the only carinomid species on the Pacific coast, but research suggests that there are likely at least four other species in the genus *Carinoma* in Coos Bay, alone (2008-2014, T. Hiebert and S. Maslakova, unpublished). Differentiating these five species based on morphology alone is currently very challenging.

One local heteronemertean, which might cause confusion is *Baseodiscus punnetti* which has many very minute eyespots, and slight, oblique cephalic grooves. Although both species flatten posteriorly, they can be differentiated from one another by the fact that *B. punnetti* can retract its head and *Carinoma* cannot. Other palaeonemerteans that are superficially similar to *C. mutabilis* are *Carinomella lactea* and *Tubulanus*

Carinoma mutabilis



1. *Carinoma mutabilis* (L:27cm) x3:
head changes shape constantly; no ocelli or cephalic grooves;
internal organs show as transverse lines; body thickened anteriorly,
flattened posteriorly, coiled (Coe, 1940).

pellucidus. They by possess lateral or cerebral sensory organs (Roe et al. 2007).

It is sometimes very difficult to distinguish among nemerteans without dissecting them because many identifying characteristics are internal and not visible. Ways in which the worms flatten, contract, and coil are useful as aids to identification of live specimens.

Ecological Information

Range: Described by Griffin from specimens collected in Puget Sound, Washington (Griffin 1898). Known range includes the Pacific coast of North America, from British Columbia to Gulf of California (Gibson 1995).

Local Distribution: Coos Bay sites include South Slough, Pony Slough and North Spit.

Habitat: Most commonly encountered in sand and sandy mud. Also found in clay (Haderlie 1975) and amongst wharf pilings (Griffin 1898).

Salinity: Estuarine.

Temperature: Latitudinal range would indicate a wide temperature tolerance.

Tidal Level: Intertidal and below (to 40 m) (Corrêa 1964).

Associates:

Abundance: Regularly encountered in South Slough, common in San Pedro Harbor, California but less abundant in San Diego, California (Coe 1905).

Life-History Information

Reproduction: Sexually mature in August (California and Puget Sound, Coe 1901, 1905). Dioecious (separate sexes), with many gametes released at once. Fertilization occurs in the water column. Development has been described for *C. tremaphorus* where eggs are 90–110 µm and surrounded by a chorion (Maslakova et al. 2004a, 2004b). *Carinoma mutabilis* larvae from ripe adults collected in January and February (Friday Harbor, WA) have been reared in the lab and the development of their protonephridia documented (Bartolomaeus et al. 2014).

Larva: Planktonic larvae of *C. tremaphorus* are uniformly ciliated, possess both apical tuft and posterior cirrus and are 150 µm in length (Coe 1943; Maslakova et al. 2004a, 2004b). Larvae of the genus *Carinoma* are distinct in having a single, mid-ventral eye that is

anterior to the mouth (Norenburg and Stricker 2002; Maslakova et al. 2004a, 2004b; Bartolomaeus et al. 2014).

Juvenile:

Longevity:

Growth Rate:

Food: A predator, *C. mutabilis* captures prey with its sticky, eversible proboscis.

Predators:

Behavior:

Bibliography

1. BARTOLOMAEUS, T., S. MASLAKOVA, and J. VON DOHREN. 2014. Protonephridia in the larvae of the paleonemertean species *Carinoma mutabilis* (Carinomidae, Nemertea) and *Cephalothrix (Procephalothrix) filiformis* (Cephalothricidae, Nemertea). *Zoomorphology*. 133:43-57.
2. COE, W. R. 1901. Papers from the Harriman Alaska Expedition xx. The Nemerteans. *Proceedings of the Washington Academy*. iii:pp. 1-110.
3. COE, W. R. 1905. Nemerteans of the west and northwest coasts of America. *Museum of Comparative Zoology, Cambridge, MA*.
4. —. 1943. Biology of the nemerteans of the Atlantic coast of North America. *Transactions of the Connecticut Academy of Arts and Sciences*. 35:129-328.
5. CORRÊA, D. D. 1964. Nemerteans from California and Oregon. *Proceedings of the California Academy of Sciences (series 4)*. 31:515-558.
6. GIBSON, R. 1995. Nemertean genera and species of the world: an annotated checklist of original names and description citation, synonyms, current taxonomic status, habitats and recorded zoogeographic distribution. *Journal of Natural History*. 29:271-562.
7. GRIFFIN, B. B. 1898. Description of some marine nemerteans of Puget Sound and Alaska. *Annals of the New York Academy of Sciences*. xi:pp. 193-218.
8. HADERLIE, E. C. 1975. Phylum Nemertea (Rhynchocoela), p. 112-

120. *In*: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
9. KAJIHARA, H., H. YAMASAKI, and S. ANDRADE. 2011. *Carinoma hamanako* sp. nov. (Nemertea: Palaeonemertea), the first representative of the genus from the northwest Pacific. *Species Diversity*. 16:149-165.
10. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent Regions. University of Washington Press, Seattle.
11. MASLAKOVA, S., and J. NORENBURG. 2001. Trochophore larva is plesiomorphic for nemerteans: evidence for prototroch in a basal nemertean *Carinoma tremaphoros* (Phylum Nemertea, Palaeonemertea). *American Zoologist*. 41: 1515-1516.
12. MASLAKOVA, S. A., M. Q. MARTINDALE, and J. L. NORENBURG. 2004. Vestigial prototroch in a basal nemertean, *Carinoma tremaphoros* (Nemertea; Palaeonemertea). *Evolution & Development*. 6:219-226.
13. ROE, P., J. L. NORENBURG, and S. MASLAKOVA. 2007. Nemertea, p. 221-233. *In*: Light and Smith manual: intertidal invertebrates from central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.

Updated 2014

Tubulanus polymorphus

An orange ribbon worm

Phylum: Nemertea
Class: Anopla
Order: Paleonemertea
Family: Tubulanidae

“Such a worm when seen crawling in long and graceful curves over the bottom in clear water earns for itself a place among the most beautiful of all marine invertebrates” (Coe 1905)

Taxonomy: *Tubulanus polymorphus* was a name assigned in unpublished work by Renier (1804). The genera *Tubulanus* and *Carinella* were described by Renier (1804) and Johnston (1833), respectively, and were synonymized by Bürger in 1904 (Gibson 1995). Melville (1986) and the International Code of Zoological Nomenclature (ICZN) determined that the family name Tubulanidae take precedence over its senior subjective synonym Carinellidae (Ritger and Norenburg 2006) and the name *Tubulanus polymorphus* was deemed published and available (ICZN 1988). Previous names for *T. polymorphus* include *C. polymorpha*, *C. rubra* and *C. speciosa*.

Description

Size: A large nemertean, up to three meters when extended. Commonly 25–75 cm in length and 5 mm in width (Coe 1901, 1905; Corrêa 1964).

Color: Individuals boldly colored in solid red, brown, orange or vermillion. No patterns and no dorsal or ventral color differences (Coe 1901).

General Morphology: Recognizable by bright orange color and long, stretchy morphology. Individuals are sometimes found within parchment tubes.

Body: Long, thin and very soft (Coe 1901). Non-segmented (phylum Nemertea), cylindrical anterior but can flatten posteriorly (Fig. 1).

Anterior: Head rather broad, set off from body and somewhat flattened. No cephalic grooves (order

Palaenemertea) but with lateral transverse grooves (Fig. 2a, b, c). Head cannot completely withdraw into body (Kozloff 1974).

Posterior: No caudal cirrus.

Eyes/Eyespots: None.

Mouth: A long slit-like opening (Fig. 2c) posterior to the brain, separate from proboscis pore (Fig. 2c) and positioned just behind transverse furrows (Coe 1901).

Proboscis: Eversible (phylum Nemertea) and, when not everted, coiled inside rhynchocoel (cavity). The proboscis in *Tubulanus polymorphus* is short with the rhynchocoel reaching one third total worm body length. Proboscis bears no stylets and the proboscis pore almost terminal (Fig. 2c).

Tube/Burrow: As is true for most *Tubulanus* species, *T. polymorphus* individuals live in thin parchment tubes that are attached to rocks or shells and made of hardened mucous secretions (Coe 1943).

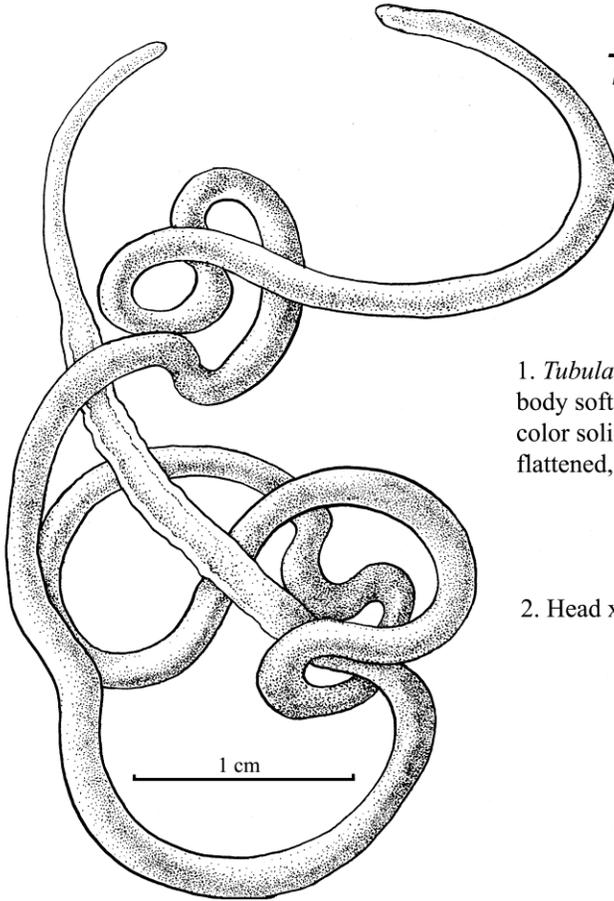
Possible Misidentifications

The genus *Tubulanus* is slender, soft, extensible without ocelli or cephalic grooves (Corrêa 1964) and with a flattened head with transverse lateral grooves. Five other species of *Tubulanus* are reported for Pacific Northwest intertidal and subtidal habitats (Roe et al. 2007). *T. polymorphus* and *T. sexlineatus* are most common intertidally. *Tubulanus polymorphus* can be distinguished from the others by its large size, strong color and lack of pattern.

Some of the other species are:

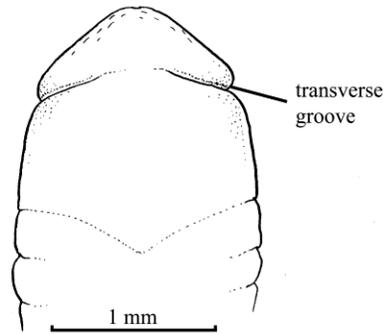
Tubulanus pellucidus, a small (to 2.5 cm in length), white to translucent tube-dweller in estuaries, occurs on the Pacific coast from San Francisco to San Diego and on the Atlantic coast from New England to Florida (Gibson 1995; Roe et al. 2007). *Tubulanus cingulatus* is deep brown with white transverse rings and four long stripes.

Tubulanus polymorphus

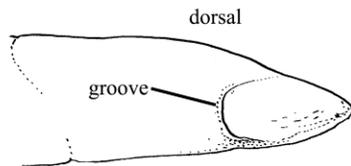


1. *Tubulanus polymorphus* (L: 25 cm) x4:
body soft, cylindrical; can be flattened posteriorly;
color solid orange, red or brown; no pattern; head
flattened, without ocelli or cephalic grooves.

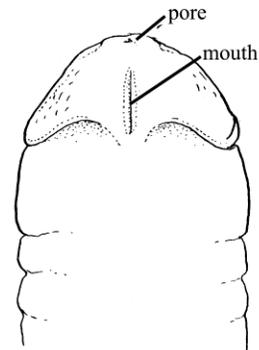
2. Head x30.



2a. (dorsal view) showing transverse
grooves; no ocelli or lateral cephalic
grooves.



2b. (lateral view) showing flattening,
transverse grooves.



2c. (ventral view) showing proboscis
pore, long, slit-like mouth, transverse grooves.

Individuals reach lengths to 15 cm and occur subtidally and lower in soft sediments. Pacific distribution from Bolinas to San Diego, California (Coe 1904; Roe et al. 2007).

Tubulanus sexlineatus is up to 1.5 m in length, chocolate brown with white rings and 5–6 longitudinal lines. This tube-dwelling species is found from Alaska to southern California (Griffin 1898; Roe et al. 2007).

Tubulanus capistratus is a slender and brown tube-dweller (Coe 1901), up to one meter long, with many narrow white transverse rings and three longitudinal lines. The range of *T. capistratus* is Alaska to Monterey Bay, California (Roe et al. 2007). Subtidal species found off the coast of southern California include *T. albocinctus* and *T. frenatus* (Coe 1904; Corrêa 1964).

Because of the many identifying characteristics that are internal and not visible, it is sometimes very difficult to distinguish among nemerteans without dissecting them. Ways in which the worms flatten, contract, and coil are useful as aids to identification of live specimens.

Ecological Information

Range: NE Pacific range Aleutian Islands, Alaska south to Monterey, California. Worldwide distribution includes northern European and Mediterranean coasts.

Local Distribution: Collected in Coos Bay in exposed parts of estuaries, as well as rocky outer shores. Coos Bay sites include Charleston, Barview and Pony Slough.

Habitat: Under heavy boulders, among mussels, in mud and shell hash, on both open coast and in bays (Haderlie 1975). It is the common large orange nemertean of the outer coastal rocky intertidal.

Salinity: Often collected on outer rocky shores at salinities of 30.

Temperature: Found in cold and temperate waters.

Tidal Level: Intertidal (Corrêa 1964) to low intertidal and subtidal zones (Haderlie 1980).

Associates: Small polychaetes are often found within the parchment tubes of *T. polymorphus*.

Abundance: Rather common (Corrêa 1964) and quite common on the outer coast in Oregon, but rarely abundant in Alaska (Coe 1901).

Life-History Information

Reproduction: Male and female individuals often inhabit the same parchment tube where they deposit eggs (Coe 1943). Specimens are sexually mature from early summer (San Juan Island, WA, Stricker 1987) to August (Coe 1905) and can produce great numbers of large (350 µm in diameter) eggs (Stricker 1987), which are often used for experimental studies (Coe 1940; Stricker et al. 2001, 2013).

Larva: Larvae hatch after two days, are large (500 µm in length) and uniformly ciliated with inconspicuous apical tuft of cilia (Stricker 1987). These lecithotrophic larvae develop rapidly (approximately 90 hr, Coe 1940; Stricker 1987).

Juvenile:

Longevity:

Growth Rate: The growth rate of most nemerteans is unknown. Most species have some regenerative ability. *Tubulanus polymorphus* and *T. sexlineatus* are known to regenerate both anterior and posterior ends (T. Hiebert, pers. obs.)

Food: A predator on soft-bodied worms and mollusks, where only soft parts are ingested from larger prey (Coe 1943).

Predators:

Behavior: Can be found at low tide searching for food.

Bibliography

1. COE, W. R. 1901. Papers from the Harriman Alaska Expedition. The Nemerteans. Proceedings of the Washington Academy:1-110.
2. —. 1904. Nemerteans of the Pacific coast of North America. Harriman Expedition. 11:111-220.
3. —. 1905. Nemerteans of the west and northwest coasts of North America. Bulletin of the Museum at Harvard College. xlvii:1-318.
4. —. 1940. Revision of the nemertean fauna of the Pacific coasts of north, central and northern South America. Allan Hancock Pacific Expeditions. Reports. 2:247-323.
5. —. 1943. Biology of the nemerteans of the Atlantic coast of North America. Transactions of the Connecticut Academy of Arts and Sciences. 35:129-328.

6. CORRÉA, D. D. 1964. Nemerteans from California and Oregon. *Proceedings of the California Academy of Sciences* (series 4). 31:515-558.
7. GIBSON, R. 1995. Nemertean genera and species of the world: an annotated checklist of original names and description citation, synonyms, current taxonomic status, habitats and recorded zoogeographic distribution. *Journal of Natural History*. 29:271-562.
8. GRIFFIN, B. B. 1898. Description of some marine Nemerteans of Puget Sound and Alaska. *Annals of the New York Academy of Sciences*. xi:pp. 193-218.
9. HADERLIE, E. C. 1975. Phylum Nemertea (Rhynchocoela), p. 112-120. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
10. —. 1980. Polychaeta: The Marine annelid worms, p. 448-489. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
11. INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1988. *Tubulanus* Renier 1804 and *Tubulanus polymorphus* Renier 1804 (Nemertea) reinstated and made available. *Bulletin of Zoological Nomenclature*. 45:157-158.
12. JOHNSTON, G. 1833. Illustrations in British zoology. *Magazine of Natural History*. 6:232-235.
13. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
14. MELVILLE, R. V. 1986. *Tubulanus* and *Tubulanus polymorphus* (Polychaeta) proposed reinstatement under plenary powers. *Bulletin of Zoological Nomenclature*. 43:112-114.
15. RITGER, R. K., and J. L. NORENBURG. 2006. *Tubulanus riceae* new species (Nemertea: Anopla: Palaeonemertea: Tubulanidae), from south Florida, Belize and Panama. *Journal of Natural History*. 40:931-942.
16. ROE, P., J. L. NORENBURG, and S. MASLAKOVA. 2007. Nemertea, p. 221-233. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
17. STRICKER, S. A. 1987. Phylum Nemertea, p. 129-137. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. University of Washington Press, Seattle, WA.
18. STRICKER, S. A., C. CLINE, and D. GOODRICH. 2013. Oocyte maturation and fertilization in marine nemertean worms: using similar sorts of signaling pathways as in mammals, but often with differing results. *Biological Bulletin*. 224:137-155.
19. STRICKER, S. A., T. L. SMYTHE, L. MILLER, and J. L. NORENBURG. 2001. Comparative biology of oogenesis in nemertean worms. *Acta Zoologica*. 82:213-230.

Updated 2014

Tubulanus sexlineatus

The six-lined ribbon worm

Phylum: Nemertea
Class: Anopla
Order: Paleonemertea
Family: Tubulanidae

Taxonomy: The genera *Tubulanus* and *Carinella* were described by Renier (1804) and Johnson (1833), respectively, and were synonymized by Bürger in 1904 (Gibson 1995). Melville (1986) and the International Code of Zoological Nomenclature determined that the family name Tubulanidae takes precedence over its senior subjective synonym Carinellidae (Ritger and Norenburg 2006). Synonyms for *T. sexlineatus* include *C. sexlineata* and *C. dinema*.

Description

Size: Individuals are 20 cm in length, on average, but can extend to 1 m (Haderlie 1975; Griffin 1898). The illustrated specimen 25 cm in length and 1.5–2 cm in width (from Coos Bay).

Color: Most commonly dark brown with more than 150 regular horizontal bands and 5–6 longitudinal lines (Coe 1905). One of these lines is mid-dorsal and two are dorso-lateral. Two are ventral, dividing ventrum into three parts (Fig. 2b). If six lines are present, the sixth is a faint mid-ventral line. Horizontal bands begin at the tip of the head and only about half of them continue down through the lateral edge to the ventrum (Fig. 3). Bands are sometimes very wide in mid-section. The longitudinal lines vary in extension and are occasionally broken into spots (Griffin 1898; Haderlie 1980).

General Morphology: Soft, elongate, non-segmented (Phylum Nemertea) (Fig. 1).

Body: Cylindrical body can be slightly flattened posteriorly (Order Paleonemertea; Heteronemertea are often flat and ribbonlike, see *Cerebratulus*).

Anterior: Head blunt, not snake-like (order Paleonemertea) and not completely retractable into body. Often flattened dorsoventrally and disc-like. Head is wider than trunk, from which it is separated by a constriction (Fig. 2b). Distinct dark cephalic furrows extend from sub-

terminal proboscis pore (Figs. 2b, 2c), and lateral transverse grooves are present just above the constriction which separates head from trunk (Fig. 2b) (Order Paleonemertea). Well-developed cerebral sense organs (sensory pits and dorsal grooves) and lateral sense organs (rounded pits next to fifth horizontal ring) (Figs. 1, 3) are present. Nephridia are well developed and exit via pores near the anterior end of the lateral sense organ (Coe 1905) (Fig. 3).

Posterior: Flattened and light in color around anal pore. No caudal cirrus (Fig. 1).

Eyes/Eyespots: No ocelli (Order Paleonemertea).

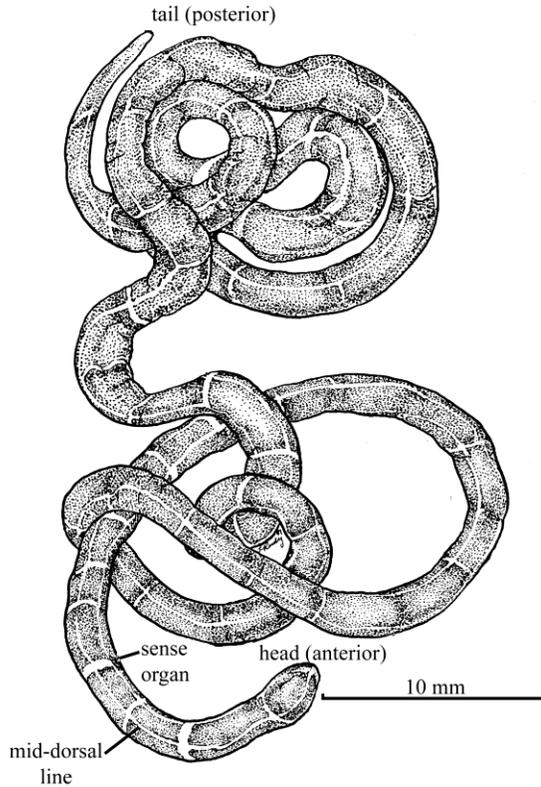
Mouth: Directly behind brain (Class Anopla) and not connected to proboscis pore. Mouth is situated ventrally just behind transverse grooves (Fig. 2b) (Haderlie 1975) and between horizontal pigment bands one and two (Griffin 1898).

Proboscis: Eversible (phylum Nemertea) and, when not everted, coiled inside rhynchocoel (cavity). Proboscis short, without stylets (class Anopla) and rhynchocoel less than half body length. Proboscis pore sub-terminal (Fig. 2b).

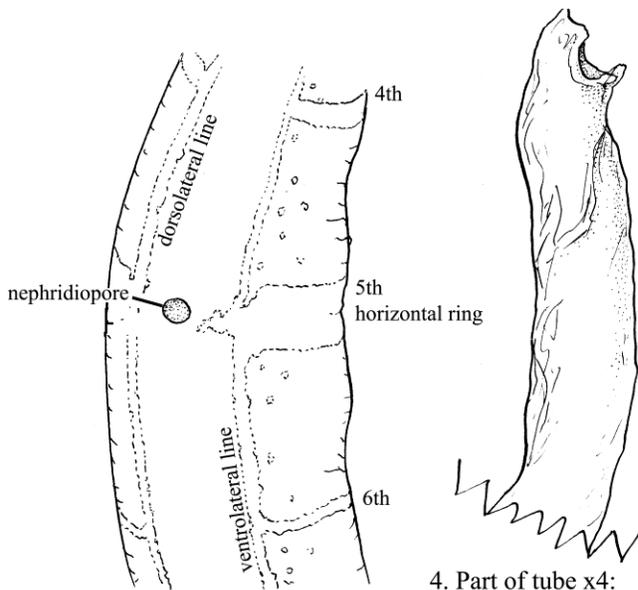
Tube/Burrow: Their long, white, rather transparent and tough tubes open at both ends (Fig. 4) and are secreted by worm's epidermis (Coe 1905).

Possible Misidentifications

The brown color of *Tubulanus sexlineatus*, with both vertical and horizontal markings, is quite distinctive, especially in nemerteans without ocelli or lateral cephalic grooves. There are several other species of *Tubulanus* in our area of which *T. sexlineatus* and *T. polymorphus* are most common and are recognizable from one another by their dramatically differing pigment. The latter species is bright orange



1. *Tubulanus sexlineatus* (L: 25cm) x4: delicate, extensible; posterior flattened; 5-6 thin white longitudinal lines, many regular horizontal rings on brown ground.

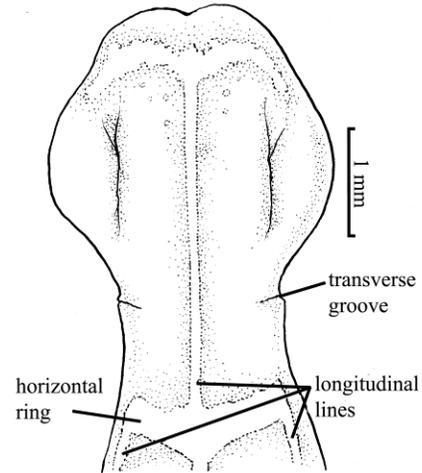


3. Lateral sensory organ.

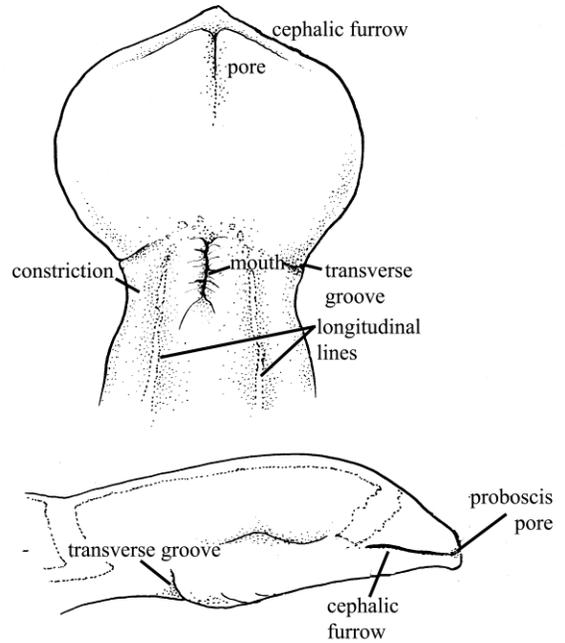
4. Part of tube x4: whitish, clear and papery.

Tubulanus sexlineatus

2a. Head (dorsal view) x20: flattened, eyeless; constriction between head and trunk; three longitudinal lines; lateral transverse grooves just anterior to constriction.



2b. Head (ventral view): proboscis pore subterminal, mouth posterior to transverse grooves.



2c. (Lateral view): cephalic furrow; no ocelli.

and lacks lines. Those with surface patterns which may provide a possible misidentification include: *T. cingulatus*, which is deep brown with white rings, but has only four longitudinal lines, not 5–6 and is subtidal; *T. capistratus*, is slender and brown with many narrow white rings but only three longitudinal lines and is up to 1 m in length; *T. albocinctus* is deep red with many narrow white rings, but without any longitudinal lines.

Because of the many identifying characteristics, which are internal and not visible, it is sometimes very difficult to distinguish among nemerteans without dissecting them. Ways in which the worms flatten, contract, and coil are useful as aids to identification of live specimens.

Ecological Information

Range: Described by Griffin from specimens collected in Puget Sound, Washington and Alaska (Griffin 1898). Known range includes Alaska to southern California (Coe 1905).

Local Distribution: Coos Bay sites in spoil islands of lower bay and the open coast of Cape Arago.

Habitat: Occurs in tubes among algae, mussels, under rocks and on pilings.

Salinity: Collected locally at salinity of 30.

Temperature:

Tidal Level: Intertidal (Coe 1905) and collected at about +0.3 m.

Associates: Found with terebellids and the polynoid polychaete, *Halosydna brevisetosa*.

Abundance: Rather common (Coe 1905).

Life-History Information

Reproduction: The reproduction and development of *T. sexlineatus* is not known.

Larva: The larval development of *T. sexlineatus* is not currently known, but is suspected to have a planktotrophic, planuliform larva (Norenburg and Stricker 2002) with lateral cirri, as is observed in other *Tubulanus* larvae (T. Hiebert, pers. obs.).

Juvenile:

Longevity:

Growth Rate: The growth rate of most nemerteans is unknown, however, most species have some regenerative ability. *Tubulanus sexlineatus* and *T. polymorphus* are known to regenerate both anterior and posterior ends (T. Hiebert, pers. obs.)

Food: Predatory on polychaetes.

Predators:

Behavior:

Bibliography

1. COE, W. R. 1905. Nemerteans of the west and northwest coasts of North America. Bulletin of the Museum at Harvard College. xlvii:1-318.
2. GIBSON, R. 1995. Nemertean genera and species of the world: an annotated checklist of original names and description citation, synonyms, current taxonomic status, habitats and recorded zoogeographic distribution. Journal of Natural History. 29:271-562.
3. GRIFFIN, B. B. 1898. Description of some marine nemerteans of Puget Sound and Alaska. Annals of the New York Academy of Sciences. xi:pp. 193-218.
4. HADERLIE, E. C. 1975. Phylum Nemertea (Rhynchocoela), p. 112-120. *In*: Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
5. —. 1980. Polychaeta: The Marine annelid worms, p. 448-489. *In*: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
6. NORENBURG, J. L., and S. A. STRICKER. 2002. Phylum Nemertea, p. 163-177. *In*: Atlas of marine invertebrate larvae. C. M. Young, M. A. Sewall, and M. E. Rice (eds.). Academic Press, San Diego, CA.
7. RITGER, R. K., and J. L. NORENBURG. 2006. *Tubulanus riceae* new species (Nemertea: Anopla: Palaeonemertea: Tubulanidae), from south Florida, Belize and Panama. Journal of Natural History. 40:931-942.

Updated 2014

T.C. Hiebert and L. Hiebert

Cerebratulus californiensis

A ribbon worm

Phylum: Nemertea
Class: Anopla
Order: Heteronemertea
Family: Lineidae

Description

Size: Up to 15 cm in length and 4–5 mm in width in posterior, flattened region (Haderlie 1980; Roe et al. 2007).

Color: Usually yellowish to rosy salmon, but may be slate colored, with paler cephalic lobe, reddish brain, conspicuous red lateral nerve cords and pale lateral margins (Haderlie 1980; Roe et al. 2007).

General Morphology:

Body: Firm, cylindrical anterior, but flattened posteriorly to aid in swimming (Haderlie 1980; Roe et al. 2007).

Anterior: Head is narrower than body with pointed snout and deep, lateral cephalic grooves (Roe et al. 2007).

Posterior: Caudal cirrus is short and often lost during collection (Fig. 1).

Eyes/Eyespots: None.

Mouth: Ventral and behind the brain, distinct from proboscis pore (order Heteronemertea) (Kozloff 1974).

Proboscis: Eversible (phylum Nemertea) and, when not everted, coiled inside rhynchocoel (cavity). Proboscis of moderately sized with bears sticky glandular surface and is everted more frequently than in *C. marginatus*. No stylet (class Anopla) (Kozloff 1974).

Tube/Burrow: An excellent swimmer and strong burrower, *C. californiensis* does not inhabit a permanent tube or burrow.

Possible Misidentifications

Eight *Cerebratulus* species are reported from central CA to OR (Roe et al. 2007). Species in this genus have firm, non-contractile and often ribbon-like bodies. One species that is easily mistaken for *C. californiensis* is *C. marginatus*. Both are slate colored and possess thin lateral margins that are colorless or white. *Cerebratulus californiensis* can be identified by a head that is smaller than the body width (compare Figs. 1a and 1b) and by thin wide margins that

span anteriorly farther than in *C. marginatus* (T. Hiebert and S. Maslakova, pers obs).

Locally, research suggests that there are at least two more *Cerebratulus* species, which are currently undescribed, and closely related to *C. californiensis* (T. Hiebert and S. Maslakova, pers obs).

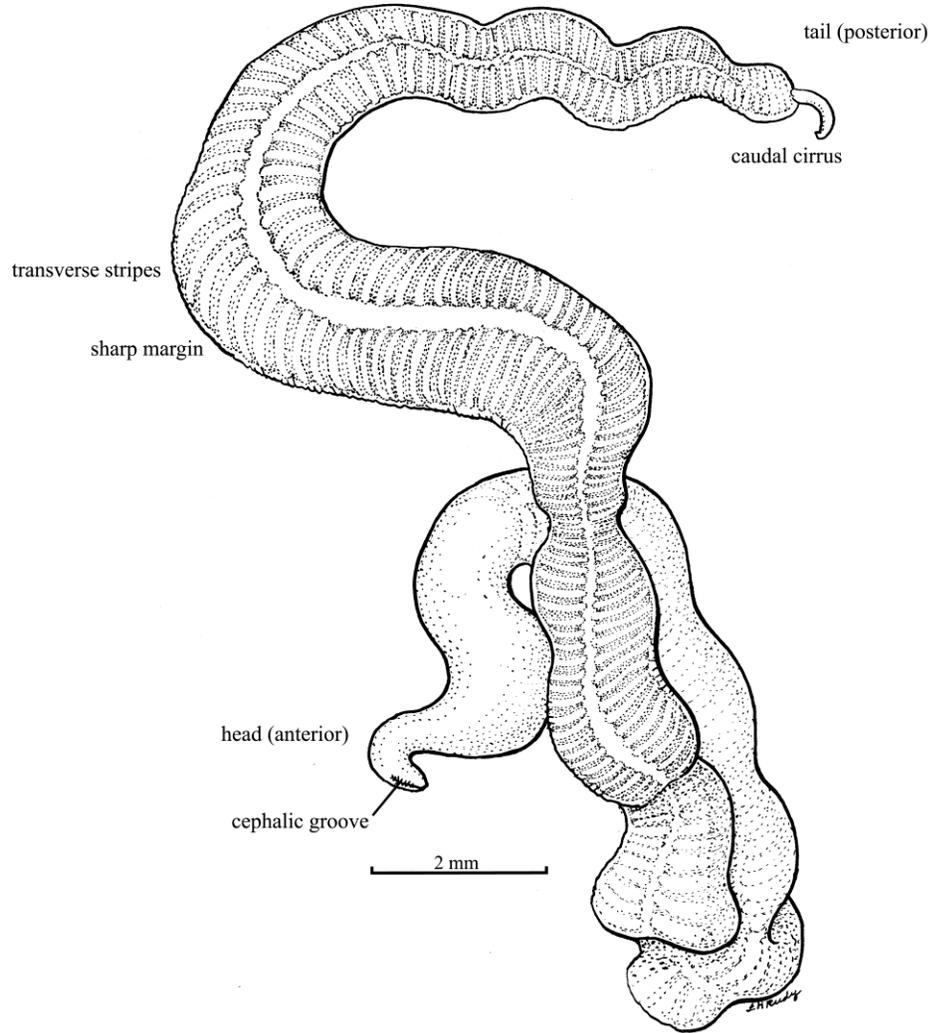
Other NE Pacific *Cerebratulus* species include: *C. albifrons*, a dark brown species with white head, up to 30 cm in length and found intertidal and subtidal in Alaska to San Diego, CA (Coe 1901; Kozloff 1974; Roe et al. 2007); *C. montgomeryi* with red body and head with white tip, occurs intertidal and subtidally from Alaska to Monterey Bay (Coe 1901); *C. occidentalis* is a subtidal species, up to 30 cm in length, reddish-brown dorsally with lighter ventral pigment, from Alaska to Puget Sound and San Francisco Bay (Coe 1901); *C. longiceps* is found in the low intertidal, dredged, is up to 30 cm in length, dark reddish-brown with pale anterior and occurs from Alaska and Tamales Bay (Coe 1901; Corrêa 1964); *C. herculeus* is enormous in size (up to 2 m long and 25 mm wide), burrows in soft sediment intertidally and subtidally from Alaska to southern California (Coe 1901); *C. lineolatus* is pale grey with olive longitudinal lines extending the entire body length (up to 20 cm) and is found intertidally up to 70 m from southern California to Mexico, and also in Miami, Florida (Coe 1905; Corrêa 1964).

Because of the many identifying characteristics, which are internal and not visible, it is sometimes very difficult to distinguish among Nemerteans without dissecting them. Ways in which the worms flatten, contract, and coil are useful as aids to identification of live specimens.

Ecological Information

Range: Described from specimens collected at San Pedro Harbor, Dead Man's Island and San Diego, California by Coe (1905). Known

Cerebratulus californiensis



1. *Cerebratulus californiensis* x15:
pale orange with white stripes, head and tail.

range includes Jalisco, Mexico to Puget Sound (Haderlie 1980).

Local Distribution: Coos Bay sites include several mudflats along South Slough and North Spit.

Habitat: Burrows in soft sediment, including sand and mudflats of bays and harbors, and sand of exposed beaches (Kozloff 1974; Haderlie 1980; Roe et al. 2007).

Salinity:

Temperature:

Tidal Level: Low intertidal zone and subtidal to at least 50 m (Gibson 1995).

Associates: Polychaetes, tanaidaceans (*Leptochelia spp.*), amphipods.

Abundance: Fairly common, but not as common as its congener, *C. marginatus*.

Life-History Information

Reproduction: Breeds in July in northern distribution, but breeding in southern California occurs in May and June (Coe 1940; Haderlie 1980).

Larva: Development is indirect with planktotrophic pilidium larval stage (Haderlie 1980). The larvae of *C. californiensis* are unique in having distinct pigment on larval lobes and lappets (Maslakova and Hiebert 2014).

Juvenile:

Longevity:

Growth Rate:

Food: Preys on polychaetes.

Predators:

Behavior: Swims with rapid dorsoventral undulations of flattened body. Frequently fragments when disturbed (Haderlie 1980; Roe et al. 2007). Regeneration of lost posterior end can occur (MacGinitie and MacGinitie 1949).

Bibliography

1. COE, W. R. 1901. Papers from the Harriman Alaska Expedition. The Nemerteans. Proceedings of the Washington Academy: 1-110.
2. —. 1905. Nemerteans of the west and northwest coasts of North America.

- Bulletin of the Museum at Harvard College. xvii: 1-318.
3. —. 1940. Revision of the nemertean fauna of the Pacific coasts of north, central and northern South America. Allan Hancock Pacific Expeditions. Reports. 2:247-323.
 4. CORRÊA, D. D. 1964. Nemerteans from California and Oregon. Proceedings of the California Academy of Sciences (series 4). 31:515-558.
 5. GIBSON, R. 1995. Nemertean genera and species of the world: an annotated checklist of original names and description citation, synonyms, current taxonomic status, habitats and recorded zoogeographic distribution. Journal of Natural History. 29:271-562.
 6. HADERLIE, E. C. 1980. Nemertea: the ribbon worms, p. 84-90. *In*: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
 7. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
 8. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 9. MASLAKOVA, S. A., and T. C. HIEBERT. 2014. From trochophore to pilidium and back again: a larva's journey. International Journal of Developmental Biology. 58:585-591.
 10. ROE, P., J. L. NORENBURG, and S. MASLAKOVA. 2007. Nemertea, p. 221-233. *In*: Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.

Updated 2014

T.C Hiebert and M. Hunt

Cerebratulus marginatus

A ribbon worm

Phylum: Nemertea
Class: Anopla
Order: Heteronemertea
Family: Lineidae

Taxonomy: *Cerebratulus marginatus* was described by Renier (1804) from Naples, Italy. This species now has a worldwide distribution and an extensive list of synonyms (see Gibson 1995). Thus it is very likely that there are several different species currently referred to as *C. marginatus* from differing regions.

Description

Size: Among the largest of local nemerteans, where sizes range from 50 cm to 1 m in length and up to 15 mm in width (Coe 1901, 1905).

Color: Slate brown, dark grey or grayish green (Coe 1901). Individuals vary in color; locally they can be very dark brown. Sometimes more pale ventrally, thin lateral margins often colorless or white (Coe 1901, 1905).

General Morphology: Large, thick and round worm anteriorly but very flat and ribbon like in mid-body. Non-segmented (phylum Nemertea).

Body: Rounded anteriorly and very dorso-ventrally flattened posteriorly with thin lateral margins in intestinal region, ribbon-like (Coe 1943) (Fig 2). Not very contractile, individuals fragment easily when handled (Roe et al. 2007).

Anterior: Head spade-shaped with pointed anterior tip (Fig. 1a), widening to just wider than or equal to body width. Cephalic grooves large and deep (Coe 1905), often flaring when swimming.

Posterior: Caudal cirrus (tail) present, thin (Coe 1943) and easily lost when collecting.

Eyes/Eyespots: No ocelli.

Mouth: Ventral and behind the brain and distinct from proboscis pore (order Heteronemertea) (Kozloff 1974).

Proboscis: Eversible (phylum Nemertea) and, when not everted, coiled inside rhynchocoel (cavity). Proboscis of moderately size with sticky glandular surface is everted less readily than in *C. californiensis*. Proboscis bears no stylet (class Anopla) (Kozloff 1974).

Tube/Burrow: An excellent swimmer and strong burrower, *C. marginatus* does not inhabit a permanent tube or burrow.

Possible Misidentifications

Eight *Cerebratulus* species are reported from central CA to OR (Roe et al. 2007). Species in this genus have firm, non-contractile and often ribbon-like bodies. One species that is easily mistaken for *C. marginatus* is *C. californiensis*. Both are slate colored and possess thin lateral margins that are colorless or white. *Cerebratulus californiensis* can be identified by a head that is smaller than the body width (compare Figs. 1a and 1b) and by thin wide margins that span anteriorly farther than in *C. marginatus* (T. Hiebert and Maslakova, pers obs).

Other NE Pacific *Cerebratulus* species include *C. albifrons*, a dark brown species with white head, up to 30 cm in length and found intertidal and subtidal in Alaska to San Diego, CA (Coe 1901; Roe et al. 2007); *C. montgomeryi* with red body and head with white tip, occurs intertidal and subtidally from Alaska to Monterey Bay (Coe 1901); *C. occidentalis* is a subtidal species, up to 30 cm in length, reddish brown dorsally with lighter ventral pigment, from Alaska to Puget Sound and San Francisco Bay (Coe 1901); *C. longiceps* is found in the low intertidal, dredged, is up to 30 cm in length, dark reddish brown with pale anterior and occurs from Alaska and Tamales Bay (Coe 1901; Corrêa 1964); *C. herculeus* is enormous in size (up to 2 m long and 25 mm wide),

Cerebratulus marginatus

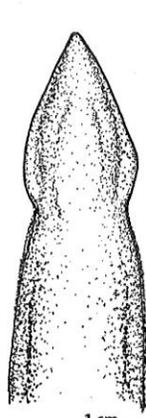


Fig 1a.
Cerebratulus marginatus anterior.



Fig 1b.
Cerebratulus californiensis
anterior.

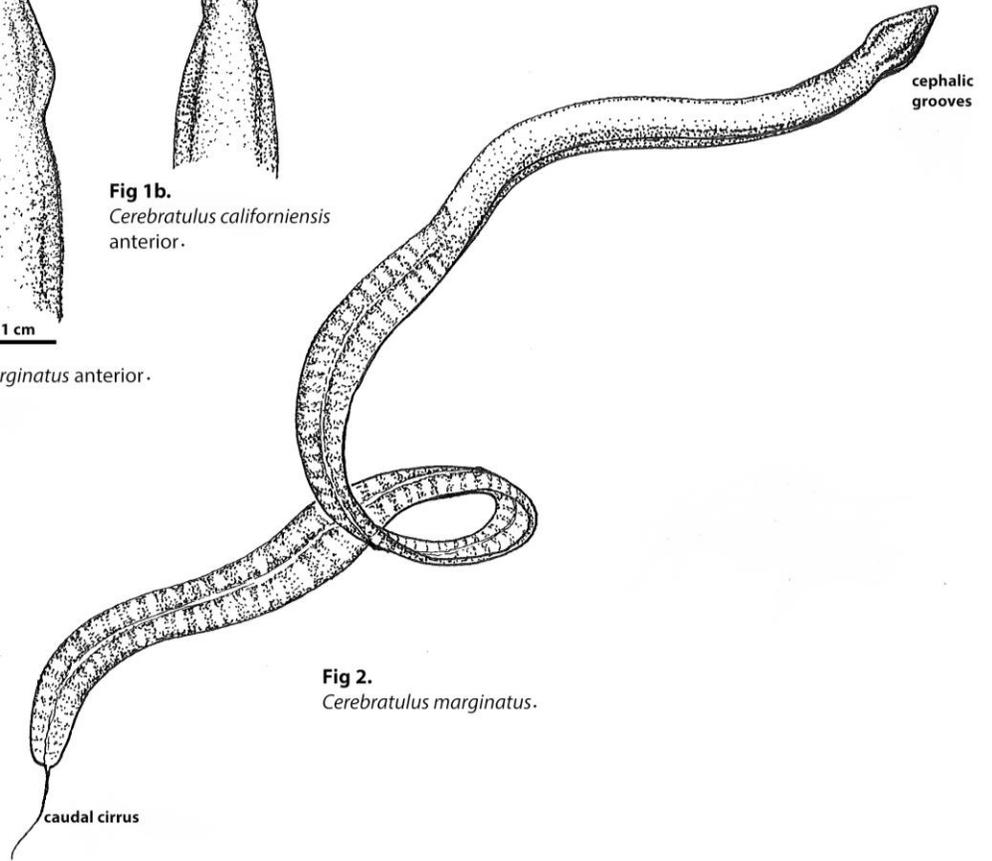


Fig 2.
Cerebratulus marginatus.

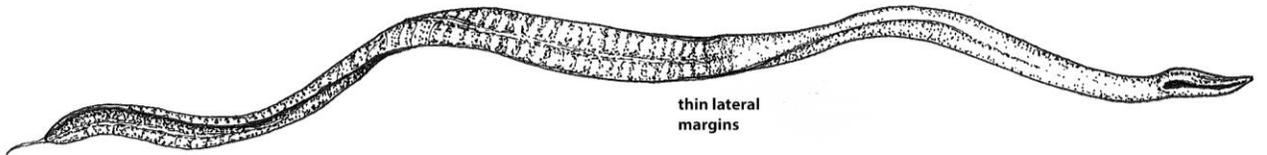


Fig 3.
Cerebratulus marginatus lateral view.

Illustration by T.C. Hiebert

burrows in soft sediment inter tidally and subtidally from Alaska to southern California (Coe 1901); *C. lineolatus* is pale grey with olive longitudinal lines extending the entire body length (up to 20 cm) and is found intertidally up to 70 m from southern California to Mexico, and also in Miami, Florida (Coe 1905; Corrêa 1964).

Because of the many identifying characteristics, which are internal and not visible, it is sometimes very difficult to distinguish among Nemerteans without dissecting them. Ways in which the worms flatten, contract, and coil are useful as aids to identification of live specimens.

Ecological Information

Range: Described from specimens in Naples, Italy (Renier 1804). The distribution of *C. marginatus* is not known with certainty as the synonymy of this species is complicated. Widespread in the northern hemisphere, Pacific coast of North America, Japan, western North Atlantic, Arctic, northern Europe including the Mediterranean (the type region). Southern distribution reaches Madeira (Gibson 1995; Roe et al. 2007).

Local Distribution: Coos Bay and South Slough, at many sites.

Habitat: Sand, mud, or fine gravel sediments (Gibson 1995).

Salinity:

Temperature: The distribution of this species suggests a wide temperature tolerance.

Tidal Level: Intertidal to sublittoral, dredged at 50 m (Coe 1905, 1940) to 150 m (Gibson 1995).

Associates:

Abundance: Frequently encountered in estuarine mudflats in Charleston, OR. Common, rendering this species useful for experimental research (e.g. Bianchi 1969; Bianchi et al. 1972; Voogt 1973).

Life-History Information

Reproduction: Males and females sexually mature in summer, gametes can be seen through body wall in serially arranged transverse lines.

Larva: A classic species for embryological work, the development of this species was documented in 1899 (Coe) and fully

described in 1930 (Schmidt) and proceeds indirectly via a planktotrophic pilidium larva (Coe 1899; Schmidt 1930; Coe 1905, 1940).

Juvenile:

Longevity:

Growth Rate:

Food: Predatory and feeds on polychaetes and clams.

Predators:

Behavior: Excellent swimmers and burrowers (Coe 1901) (Fig 3), individuals sometimes collected by net swimming at night (Coe 1943; Gibson 1995).

Bibliography

1. BIANCHI, S. 1969. Histochemistry of neurosecretory system in *Cerebratulus marginatus* (Heteronemertini). *General and Comparative Endocrinology*. 13:206-213.
2. BIANCHI, S., V. ESPOSITO, and N. GRANATA. 1972. Cerebral organs of *Cerebratulus marginatus* (Heteronemertini). *General and Comparative Endocrinology*. 18:5-20.
3. COE, W. R. 1899. On the development of the Pilidium of certain Nemerteans. *Transactions of the Connecticut Academy*. x:235-262.
4. —. 1901. Papers from the Harriman Alaska Expedition. The Nemerteans. *Proceedings of the Washington Academy*:1-110.
5. —. 1905. Nemerteans of the west and northwest coasts of North America. *Bulletin of the Museum at Harvard College*. xlvii:1-318.
6. —. 1940. Revision of the nemertean fauna of the Pacific coasts of north, central and northern South America. *Allan Hancock Foundation of Scientific Research. Allan Hancock Pacific Expeditions. Reports*. 2:247-323.
7. —. 1943. Biology of the nemerteans of the Atlantic coast of North America. *Transactions of the Connecticut Academy of Arts and Sciences*. 35:129-328.
8. CORRÊA, D. D. 1964. Nemerteans from California and Oregon. *Proceedings of the California*

- Academy of Sciences (series 4).
31:515-558.
9. GIBSON, R. 1995. Nemertean genera and species of the world: an annotated checklist of original names and description citation, synonyms, current taxonomic status, habitats and recorded zoogeographic distribution. *Journal of Natural History*. 29:271-562.
 10. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
 11. ROE, P., J. L. NORENBURG, and S. MASLAKOVA. 2007. Nemertea, p. 221-233. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 12. SCHMIDT, G. A. 1937. Bau und Entwicklung der pilidien von *Cerebratulus pantherinus* und *marginatus* und die frage der morphologischen merkmale der hauptformen der pilidien. *Zoologische Jahrbuecher Jena Anatomie*. 62:423-448.
 13. VOOGT, P. A. 1973. Biosynthesis and composition of sterols in nemertean *Cerebratulus marginatus*. *Archives Internationales De Physiologie De Biochimie Et De Biophysique*. 81:871-880.

Updated 2014

Ramphogordius sanguineus

Phylum: Nemertea
Class: Anopla
Order: Heteronemertea
Family: Lineidae

Taxonomy: The species now known as *Ramphogordius sanguineus* was originally described as *Planaria sanguinea* in 1799 by Rathke. It was transferred to the genus *Lineus* (*L. sanguineus*) by McIntosh in 1873 and has been synonymized with several lineid taxa since then, including *L. nigricans*, *L. socialis*, *L. ruber*, *L. vegetus* and *L. pseudolactues* (Bierne et al. 1993; Riser 1994). Riser (1994) designated the genus *Myoisophagos* for *L. lacteus*, *L. pseudolacteus* and *L. sanguineus*, a genus name which was later determined to be invalid and species were reassigned to the genus *Ramphogordius* (Riser 1998; Runnels 2013).

Description

Size: Individuals 0.5–15 cm in length (Roe et al. 2007) and 0.5–2 mm in width (Coe 1943; Riser 1994).

Color: Smaller individuals tend to be whitish grey, while larger ones are variously olive, red, brown, or green (Coe 1943; Riser 1994). The brain region is reddish, and the posterior end is often paler than the rest of the body (Caplins 2011). Color variance may be attributed to diet (Riser 1994). No distinct pattern, but pale circumferential rings may give segmented appearance (Roe et al. 2007).

General Morphology: Long and narrow, reddish color and head that is not distinctly marked from the rest of the body. Common under rocks.

Body: Soft and slender and non-segmented (phylum Nemertea). Coils rather than contracts when disturbed (Roe et al. 2007).

Anterior: Head with pale edges and long cephalic grooves along either side (Coe 1943; Riser 1994).

Trunk:

Posterior: No caudal cirrus.

Eyes/Eyespots: Three to eight reddish brown ocelli present within both cephalic grooves, but not necessarily in equal numbers on each side (Coe 1943; Riser 1994;

Hayward 1995; Roe et al. 2007; Caplins 2011).

Mouth: Ventral and behind the brain and distinct from proboscis pore (order Heteronemertea) (Kozloff 1974).

Proboscis: Eversible (phylum Nemertea) and, when not everted, coiled inside rhynchocoel (cavity). Proboscis wraps around prey, possibly delivering an immobilizing toxin (Caplins 2011) and is also everted when disturbed.

Tube/Burrow: None.

Possible Misidentifications

Ramphogordius sanguineus is the only member of this genus known to exist locally (Roe et al. 2007). However, the morphology of this species is similar to that of other local members of the genus *Lineus*. *Lineus ruber* is similar in color, but *R. sanguineus* is more slender when stretched, and coils spirally rather than contracting linearly when disturbed (Roe et al. 2007). *Lineus viridis* is also similar in color, but does not coil (Caplins 2011). *Lineus vegetus* may be red, green or brown in color (Kozloff 1974), has faint rings around the body, faint longitudinal lines (ibid), and coils. It extends south to Mexico (Corrêa 1964). *Lineus pictifrons* can be reddish to deep brown with a paler posterior end and is up to 12 cm in length and 3 mm in width, but has numerous yellow rings and longitudinal yellow lines, as well as two orange spots on the snout (Corrêa 1964). Its range is from Puget Sound to Mexico (ibid). *Lineus bilineatus* is dark brown or olive but has a yellow or white stripe (ibid). *Lineus torquatus* is dark reddish brown or purple with a single narrow whitish band connecting the posterior ends of its cephalic furrows. It is intertidal and occurs from Alaska to San Francisco, California (ibid). Finally, *L. flavescens* is small (8–120 mm), yellowish, pale yellow and orange, or ochre with pale head margins and 3–7 irregular red, purple or black ocelli, the largest being most anterior (Roe et al. 2007).

Ramphogordius sanguineus

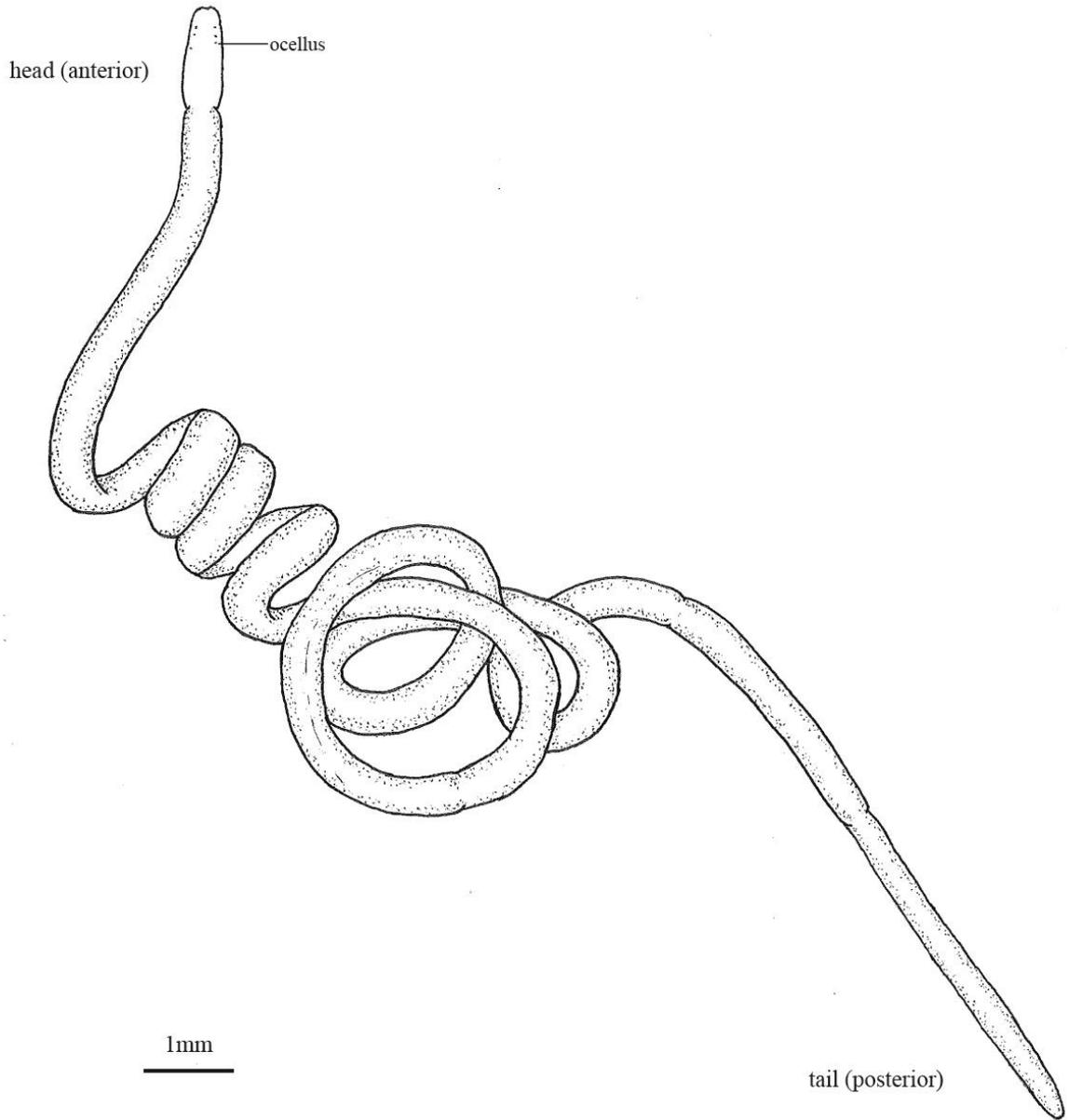


Illustration by M. Hunt

Because of the many identifying characteristics, which are internal and not visible, it is sometimes very difficult to distinguish among nemerteans without dissecting them. Ways in which the worms flatten, contract, and coil are useful as aids to identification of live specimens.

Ecological Information

Range: Range Atlantic and Pacific coasts of North America, Europe and Asia (Coe 1943; Riser 1994). Wide distribution likely due to transport in fouling communities on ships (Riser 1994). NE Pacific distribution includes California to Washington State (Roe et al. 2007).

Local Distribution: Coos Bay sites include Hayne's Inlet, the Charleston boat basin and various mudflats along the South Slough as well as coves of Cape Arago.

Habitat: Temperate subtidal and intertidal zones under rocks in sand, among rocks exposed to surf, in black mud with algae and other cover, or in mussel or oyster beds (Coe 1943; Riser 1994; Roe et al 2007; Caplins 2011). Also, found on submerged wood, buoys, and boat bottoms (Riser 1994; Caplins 2011). They frequently occur in intertwined clusters of many individuals (Roe et al. 2007).

Salinity: Tolerant of gradual salinity changes (Riser 1994).

Temperature: Tolerant of gradual thermal changes (Riser 1994).

Tidal Level: Intertidal, especially above mid-intertidal to high marsh tide pools (Roe et al. 2007).

Associates: Frequently found among mussels and oysters, and often with amphipods, annelids, and other nemerteans (Coe 1943; Riser 1994; Caplins 2011).

Abundance: Common throughout range.

Life-History Information

Reproduction: Asexual by spontaneous fragmentation (fissiparous) which is sometimes instigated by adverse conditions. Regeneration occurs in fragments containing a portion of the lateral nerve cords (Coe 1930, 1931, 1943; Riser 1994; Roe et al. 2007). Encystment often occurs, possibly as protection against predators and parasites during regeneration (Coe 1930, 1943), or to enable dispersal by currents (Caplins 2011). Sexual reproduction has not been

conclusively observed, although individuals have been collected seemingly ripe with male or female gametes (T.Hiebert and Malsakova, pers. obs).

Larva: Presence of a free-swimming larval stage is unknown (Caplins 2011).

Juvenile:

Longevity:

Growth Rate:

Food: Carnivorous, feeding on protozoans and other microfauna of lesser or comparable size (Van Guelpen 2005). Under laboratory conditions individuals will eat dead shrimp, minced clams, polychaetes, and oligochaetes (Roe et al. 2007).

Predators:

Behavior: Tends to coil into a tight spiral when disturbed (Coe 1943; Riser 1994; Roe et al. 2007).

Bibliography

1. BIERNE, J., M. TARPIN, and G. VERNET. 1993. A reassessment of the systematics and a proposal for the phylogeny of some cosmopolitan *Lineus* species (Nemertean). *Hydrobiologia*. 266:159-168.
2. CAPLINS, S. A., and J. M. TURBEVILLE. 2011. The occurrence of *Ramphogordius sanguineus* (Nemertea, Heteronemertea) in the intertidal zone of the Atlantic coast of Virginia and new observations on its feeding behavior. *Banisteria*. 38:65-70.
3. COE, W. R. 1930. Regeneration in Nemerteans. II. Regeneration of small sections of the body split or partially split longitudinally. *Journal of Experimental Zoology*. 57:109-144.
4. —. 1931. A new species of nemertean (*Lineus vegetus*) with asexual reproduction. *Zoologische Anzeiger*. 94:54-60.
5. —. 1943. Biology of the nemerteans of the Atlantic coast of North America. *Transactions of the Connecticut Academy of Arts and Sciences*. 35:129-328.
6. CORRÉA, D. D. 1964. Nemerteans from California and Oregon. *Proceedings of the California Academy of Sciences (series 4)*. 31:515-558.

7. GIBSON, R., and E. W. KNIGHT-JONES. 1995. Flatworms and ribbon worms (Phyla Platyhelminthes and Nemertea), p. 136-164. *In*: Handbook of the marine fauna of north-west Europe. P. J. Hayward and J. S. Ryland (eds.). Oxford University Press, New York.
8. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
9. RISER, N. W. 1994. The morphology and generic relationships of some fissiparous Heteronemertines. *Proceedings of the Biological Society of Washington*. 107:548-556.
10. —. 1998. The morphology of *Micrura leidyi* (Verrill, 1892) with consequent systematic reevaluation. *Hydrobiologia*. 365:149-156.
11. ROE, P., J. L. NORENBURG, and S. MASLAKOVA. 2007. Nemertea, p. 221-233. *In*: Light and Smith manual: intertidal invertebrates from central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.
12. RUNNELS, C. 2013. Phylogeography and species status of *Ramphogordius sanguineus*. M.S. Virginia Commonwealth University.
13. VAN GUELPEN, L. G., G. POHLE, E. VANDEN BERGHE, and M. J. COSTELLO. Marine species registers for the North Atlantic Ocean. <http://www.marinebiodiversity.ca/nonNARMS>.

Updated 2014

T.C. Hiebert and M. Hunt

Amphiporus imparispinosus

Phylum: Nemertea
Class: Enopla
Order: Hoplonemertea, Monostylitera
Family: Amphiporidae

Taxonomy: Overlapping species ranges and suggested synonymy exists between *A. imparispinosus* and *A. similis* (= *A. imparispinosus* var. *similis*) and *A. leuciodus* (Coe 1901, 1905). For this reason, *A. imparispinosus* is indicated as *species inquirenda* (identity requires further investigation) (Gibson and Crandall 1989; Gibson 1995).

Description

Size: Individuals are 25–50 mm in length and very slender (Coe 1905).

Color: Solid, opaque-white and sometimes pale reddish with yellowish tinge. Also pale yellow or flesh-colored. The brain area is pink and intestinal canal brownish (Coe 1905).

General Morphology: Soft, elongate and not segmented (phylum Nemertea).

Body: Long and slender, especially for the family Amphiporidae, and slightly flattened posteriorly (Fig. 1).

Anterior: Head not strongly differentiated from rest of body (Fig. 2).

Posterior: Tapers to a blunt end. No caudal cirrus (Fig. 1).

Eyes/Eyespots: Many, small eyes present in two groups on each side of the head and are positioned anterior to brain. The first is an elongated group of 6–15 ocelli found along the anterior margin. The second, a posterior group of about the same number, (but it can be up to 30) which is internal to the first group. Fewer eyes are present in younger animals (Fig. 2).

Mouth: Anterior to brain opens into proboscis pore (class Enopla) (Corrêa 1964).

Proboscis: Very long and contained within a muscular sheath (rhyngocoel) which is almost as long as the total body length (genus *Amphiporus*). The proboscis is armed with a single stylet (suborder Monostylifera), in which the proximal end of the basal segment is rounded and wide (Fig. 3). Three accessory stylet pouches are present, each containing two or more reserve stylets (Griffin 1898;

Corrêa 1964; Stricker and Cloney 1982). (The proboscis must be everted or the worm dissected to see the stylet and pouches.)

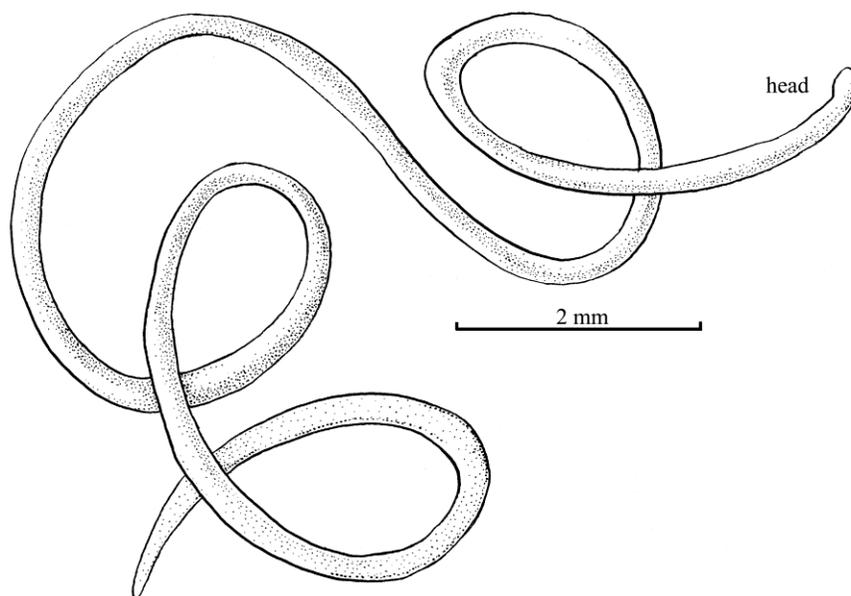
Tube/Burrow: *Amphiporus imparispinosus* does not inhabit a tube.

Possible Misidentifications

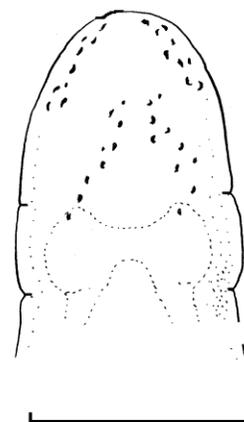
The locally represented (central CA to OR, Roe et al. 2007) hoplonemerteans (the free-living Enopla), with a central proboscis stylet (suborder Monostylifera), can be divided into ten families (Chernyshev 2005). 1) The Ototyphlonemertidae have no ocelli as adults and possess statocysts; 2) the Emplectonometatidae have a short proboscis, usually numerous ocelli (four or more); 3) the Prosorhochmididae have a very long, slender proboscis, usually two pairs of large ocelli and a distinctive smile-like fold on the head (the “smiling worms”, Maslakova and Norenburg 2008); 4) The Tetrastematidae usually have four ocelli and are small or medium-sized nemerteans; 5) The Carcinonemertidae are small nemerteans with 0–2 eyes and are parasitic on decapod crustaceans; 6) Neesidae (e.g. *Paranemertes*) and 7) Zygonemertidae are medium to large nemerteans with numerous eyes; 8) Malacobdellidae include local species which are commensal within the mantle cavity of bivalves; 9) Oerstedidae, consisting of a single local species, are small with four eyes that can be doubled (Chernyshev 2005); 10) the Amphiporidae have many eyes and are relatively short and broad although *A. imparispinosus* is unusual in this respect (Coe 1940).

There are at least eight species of *Amphiporus* reported in the Pacific Northwest, but there are likely more (Roe et al. 2007). *Amphiporus formidabilis* is the only other slender species that resembles *A. imparispinosus* superficially, and can be differentiable by 6–12 pouches of accessory stylets, where *A. imparispinosus* has 2–3. It is also much larger than *A. imparispinosus*, 10–30 cm in length (Haderlie 1975). The

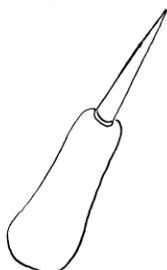
Amphiporus imparispinosus



1. *Amphiporus imparispinosus* (L: 30 mm) x20:
body long and slender, head not set off from body; solid
color, whitish; dark intestinal area; no caudal cirrus.



2. Head x35:
ocelli arranged in two groups,
one along anterior margin and the
second interior (Coe, 1905).



3. Stylet and base (proboscis) x200:
basal segment rounded (Coe, 1905).

other species are rather stout and more strongly colored. *Amphiporus rubellus* is a uniform red or orange with no pattern and 10–20 ocelli on each side of its head.

Amphiporus punctulatus is dark brown, irregularly blotched on its dorsal surface, and with a lighter head marked with two dark spots. *Amphiporus bimaculatus* (= *Nipponnemertes bimaculatus*) gets its name from the same sort of strong spots (which are not ocelli) on its light-colored head. Its general coloration is homogenous, not blotchy as in *A. punctulatus*. *Amphipours bimaculatus* secretes great quantities of mucus when disturbed (Haderlie 1980) and is known to readily evert its proboscis. A variety of *A. imparispinosus* (*A. i. similis*, Coe, 1905) varies only by having two pouches of accessory stylets not three (Coe 1940).

Because of the many identifying characteristics which are internal and not visible, it is sometimes very difficult to distinguish among nemerteans without dissecting them. Ways in which the worms flatten, contract, and coil are useful as aids to identification of live specimens.

Ecological Information

Range: Originally described from specimens collected in Puget Sound, Washington and Alaska (Griffin 1898). Known northeastern Pacific range from Siberia, Bering Sea and south to Ensenada, Mexico. *Amphiporus* is particularly rare in the tropics (Coe 1940).

Local Distribution: Coos Bay distribution at several mudflats along the South Slough and also open coast sites at Cape Arago.

Habitat: Among algae (e.g. red alga, *Corallina vancouveriensis*) shells, mussels and other growths on rocks. Individuals can exist in very exposed and surf-swept shores (Coe 1940).

Salinity: Found on the open coast, at salinities of 30.

Temperature: Latitudinal range would indicate a wide temperature tolerance, for example 10–20° C (San Pedro, CA.) to just above freezing (Bering Strait, AK).

Tidal Level: Intertidal and below to 50 m (Corrêa 1964).

Associates:

Abundance: One of the most common local *Amphiporus* species (Haderlie 1980).

Life-History Information

Reproduction: The development of *A. imparispinosus* is not known. However, individuals are likely dioecious (separate sexes) (Coe 1905) and some hoplonemerteans are hermaphroditic, with eggs and sperm released at same time. Ripe specimens of the congener, *A. formidabilis*, have been observed in winter and spring months (Washington, Stricker 1987) where oocytes were 250–350 µm in diameter surrounded by thick (up to 100 µm thick) egg jelly. Embryos cleave after six hours, develop into morulae at 20 hours and are ciliated and swimming at 42 hours (9° C, Stricker 1987)

Larva: Planuliform and lecithotrophic *A. formidabilis* larvae have an apical tuft and swim for one day before settlement (9° C, Stricker 1987).

Juvenile:

Longevity:

Growth Rate:

Food: Predatory, killing prey with an armed proboscis that secretes toxins (Bacq 1936) and kills prey before ingestion (Jennings and Gibson 1969).

Predators:

Behavior: Does not swim or roll up spirally (genus *Amphiporus*) (Coe 1905).

Bibliography

1. BACQ, Z. M. 1936. Le poisons des nemertiens. Bulletin of the Academie Royale de Belgique. Classe des Sciences. 5:1072-1079.
2. CHERNYSHEV, A. V. 2005. System of families of enoplan nemerteans of the order Eumonostilifera (Nemertea: Enopla). Russian Journal of Marine Biology. 31:S27-S33.
3. COE, W. R. 1901. Papers from the Harriman Alaska Expedition. The Nemerteans. Proceedings of the Washington Academy: 1-110.
4. —. 1905. Nemerteans of the west and northwest coasts of North America. Bulletin of the Museum at Harvard College. xlvii:1-318.
5. —. 1940. Revision of the nemertean fauna of the Pacific coasts of north,

- central and northern South America. Allan Hancock Pacific Expeditions. Reports. 2:247-323.
6. CORRÊA, D. D. 1964. Nemerteans from California and Oregon. Proceedings of the California Academy of Sciences (series 4). 31:515-558.
 7. GIBSON, R. 1995. Nemertean genera and species of the world: an annotated checklist of original names and description citation, synonyms, current taxonomic status, habitats and recorded zoogeographic distribution. Journal of Natural History. 29:271-562.
 8. GIBSON, R., and F. B. CRANDALL. 1989. The genus *Amphiporus* Ehrenberg (Nemertea, Enopla, Monostiliferoidea). Zoologica Scripta. 18:453-470.
 9. GRIFFIN, B. B. 1898. Description of some marine nemerteans of Puget Sound and Alaska. Annals of the New York Academy of Sciences. xi:pp. 193-218.
 10. HADERLIE, E. C. 1975. Phylum Nemertea (Rhynchocoela), p. 112-120. *In*: Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
 11. —. 1980. Polychaeta: The Marine annelid worms, p. 448-489. *In*: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
 12. JENNINGS, J. B., and R. GIBSON. 1969. Observations on the nutrition of seven species of Rhynchocoelan worms. Biological Bulletin. 136:405-433.
 13. MASLAKOVA, S. A., and J. L. NORENBURG. 2008. Revision of the smiling worms, genus *Prosorhochmus* Keferstein, 1862, and description of a new species, *Prosorhochmus belizeanus* sp. nov. (Prosorhochmidae, Hoplonemertea, Nemertea) from Florida and Belize. Journal of Natural History. 42:1219-1260.
 14. ROE, P., J. L. NORENBURG, and S. MASLAKOVA. 2007. Nemertea, p. 221-233. *In*: Light and Smith manual: intertidal invertebrates from Central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 15. STRICKER, S. A. 1987. Phylum Nemertea, p. 129-137. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. University of Washington Press, Seattle, WA.
 16. STRICKER, S. A., and R. A. CLONEY. 1982. Stylet formation in nemerteans. The Biological Bulletin. 162:387-403.

Updated 2014

Paranemertes peregrina

"The wanderer"

Phylum: Nemertea

Class: Enopla

Order: Hoplonemertea, Monostylifera

Family: Emplectomenatidae

Taxonomy: Coe (1905) found two morphotypes within *Paranemertes peregrina* (var. *alaskensis*, var. *californiensis*) that differed in size, color and stylet morphology (Roe et al. 2007). Whether these morphotypes represent two difference species or intraspecific divergence is currently unknown.

Description

Size: Individuals vary in size from 2–40 cm with average size range 15–25 cm (Coe 1901; Roe et al. 2007). Northern specimens (var. *alaskensis*, 40 cm) larger than southern ones (var. *californiensis*, 10 cm) (Coe 1905).

Color: Dark dorsally, purple or olive green with head brown. Lighter ventrally, white or pale yellow with mid-ventral section sometimes lighter than the rest. No lines or other patterns, except V-shape behind head.

General Morphology: Long and slender

Body: Elongate, contractile and non-segmented (phylum Nemertea). Body soft but muscular and can lengthen and shorten easily (Kozloff 1974).

Anterior: Head usually truncate, a little larger than body immediately posterior (Coe 1901). No cephalic grooves. A distinct narrow v-shaped marking just back of the head, but sometimes quite faint. A pair of white transverse lines are apparent on the lateral anterior-most margins (Fig. 2) (Kozloff 1974).

Posterior: No caudal cirrus.

Eyes/Eyespots: Two groups on each side of head consist of 5–12 minute ocelli. The first group is anterior and arranged along the antero-lateral margins and the second is irregular and near the brain (Fig. 2) (Coe 1901).

Mouth: In front of brain and united with proboscis pore (suborder Monostylifera).

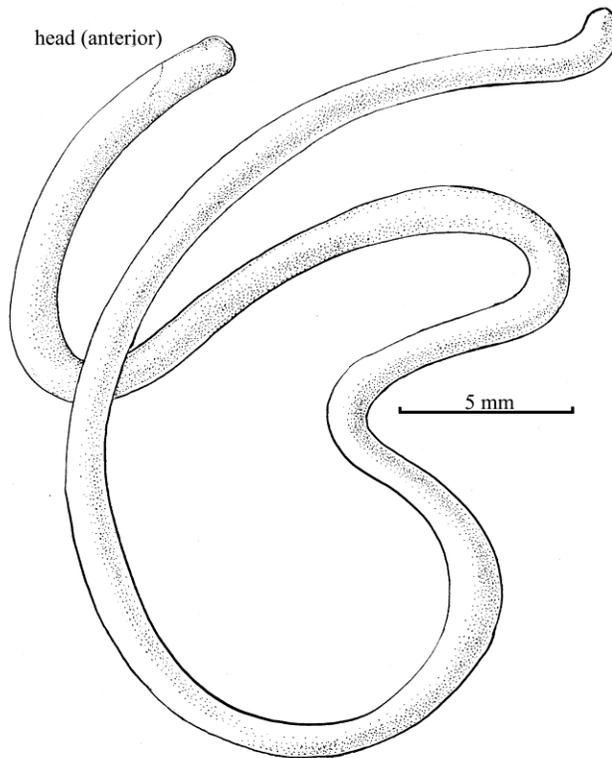
Proboscis: Eversible (phylum Nemertea) and, when not everted, coiled inside rhynchocoel (cavity). Rhynchocoel half to three-quarters body length (genus *Paranemertes*). Proboscis whitish with one (suborder Monostylifera) short, stylet (order Hoplonemertea) of lengths 85–90 µm (Coe 1905; Stricker and Cloney 1981). Stylet sculpture is variable and is either with (var. *californiensis*) (Fig. 4) or without spiral grooves (var. *alaskensis*) (Roe et al. 2007). Two (var. *californiensis*) to four (var. *alaskensis*) pouches of accessory stylets are present, each pouch with 6–10 stylets (Fig. 3) (Roe et al. 2007). Proboscis eversion can be induced with fresh water or dilute acetic acid (Haderlie 1980).

Possible Misidentifications

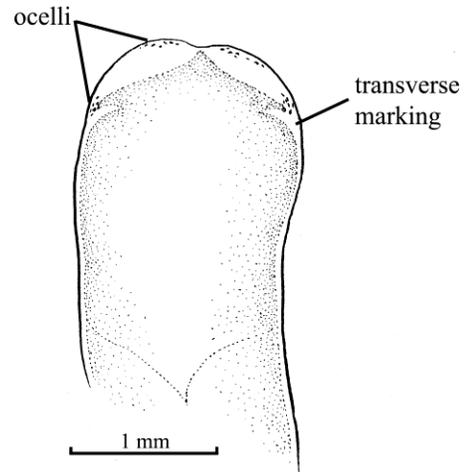
There are five genera of the family *Emplectonematidae* on the Pacific coast, all of which have a short proboscis, numerous ocelli and a long, slender body. They are each easily differentiable from the genus *Paranemertes*: *Carcinonemertes* is parasitic on crabs; *Emplectonema* is very slender with 12–14 eyes in each of two rows; *Nemertopsis* and *Dichonemertes* have only four ocelli (Coe 1940).

Of the five known Pacific species of *Paranemertes*, none is as common as *P. peregrina*. *Paranemertes pallida* has been found only in Alaska (Coe 1901). *Paranemertes carnea*, with six accessory stylet pouches, is whitish, pink, or flesh-colored, and is reported only from Alaska to Puget Sound (Coe 1901). *Paranemertes californica* is pale gray or orange anteriorly and gray or salmon posteriorly, where exterior pigmentation is often obscured by its green digestive tract, and has not been found north of Monterey Bay (Coe 1904). *Paranemertes sanjuanensis* is beige in color with five stylet pouches having two to three stylets each (Stricker 1982). Stylets are spiraled as in *P.*

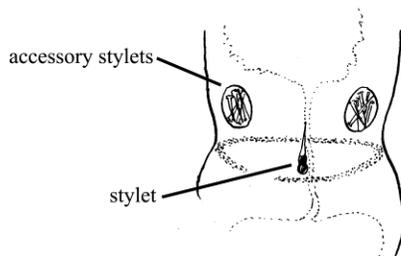
Paranemertes peregrina



1. *Paranemertes peregrina* x6:
long, slender; dark dorsally; no cephalic grooves or caudal cirrus; solid color, no patterns; narrow, v-shaped marking behind head.



2. Head (dorsal view) x25:
a pair of transverse lateral white markings; two groups of 5-12 ocelli near anterior edge, two groups farther back; light ventral color shows at edges.



3. Stylet area, proboscis:
everted; central stylet and two pouches of accessory stylets (Coe, 1905).



4. Central stylet and base showing spiral grooves (var. *californiensis* Coe 1905, Gibson 1973).

peregrina with which it co-occurs. Range San Juan Island, WA to Bodega Bay, CA (Roe et al. 2007).

Ecological Information

Range: Bering Sea, AK to southern California where it is widely distributed in many habitats.

Local Distribution: Coos Bay sites include Barview, North South Slough, Haynes Inlet, Kentuck Inlet, South Slough and Charleston as well as rocky outer shores.

Habitat: Found under a great variety of conditions, on rocky shores and mudflats and amongst mussel beds, seaweeds, coralline algae. Avoids bright light.

Salinity: Individuals collected in estuarine habitats as well as open coast at salinities of 30.

Temperature: The wide distribution range would indicate a tolerance of very cold to temperate conditions.

Tidal Level: Intertidal and below.

Associates:

Abundance: Common in many habitats with a maximum average density of 14 worms/m² (Coe 1905), usually less (Haderlie 1975; Roe 1979). Easily the most common mudflat nemertean at Charleston.

Life-History Information

Reproduction: Females may outnumber males in some populations (Washington, Haderlie 1980). Spawning occurs in spring and summer and eggs take up to six months to mature. Eggs are yellow to pinkish in color and approximately 250 µm in diameter and are surrounded by a large egg chorion (Maslakova and von Döhren 2009; T. Hiebert pers. obs). Deposits of single or gelatinous clusters of many fertilized eggs can be found in the warmer months (Coe 1940).

Larva: Lecithotrophic larvae hatch two to three days after fertilization and deposition of the eggs, are bullet-shaped, uniformly ciliated and possess an apical tuft of longer cilia and 4–6 ocelli and are planktonic for 3–8 weeks (Roe 1976; Malskova and von Döhren 2009).

Juvenile:

Longevity: 1.5 to 1.75 years where adults may spawn three times (Roe 1976; Haderlie 1980).

Growth Rate:

Food: Diet consists almost entirely of nereid worms. Although individuals will occasionally eat the polychaete *Polydora* sp.

Paranemertes peregrina eats *Nereis vexillosa* and appears to prefer the small, timid *Platynereis bicanaliculata*, which lives in tubes on *Ulva* sp. (Puget Sound). Some syllid polychaetes are partly immune to the venom of *Paranemertes peregrina* (Roe 1971).

Predators: Crabs will eat nemerteans only if very hungry and after first cleaning off the mucus with their claws (Gibson 1972).

Behavior: A diurnal feeder, *P. peregrina* is well known as a voracious, aggressive hunter. It conducts its haphazard searches when the tide is out and nereids are unable to escape. Individuals are most abundant as the tide recedes. On cloudy days, individuals have a temporary burrow to which they retreats on a slime track (Kozloff 1974). Its predatory attacks may involve chemoreception (Amerongen and Chia 1982). During an attack, its proboscis wraps around the prey (e.g., a nereid) and it emits a venomous mucus (toxin anabaseine) (Gibson 1970; Roe 1971), which stuns the prey for about 20 minutes (Roe 1971). The proboscis then withdraws, drawing the prey into the mouth. Worms of a great length can be eaten by *P. peregrina*, but not those of a large diameter.

Bibliography

1. AMERONGEN, H. M., and F. S. CHIA. 1982. Behavioral evidence for a chemoreceptive function of the cerebral organs in *Paranemertes peregrina* Coe (Hoplonemertea, Monostilifera). *Journal of Experimental Marine Biology and Ecology*. 64:11-16.
2. COE, W. R. 1901. Papers from the Harriman Alaska Expedition. The Nemerteans. *Proceedings of the Washington Academy*: 1-110.
3. —. 1904. Nemerteans of the Pacific coast of North America. *Harriman Expedition*. 11:111-220.
4. —. 1905. Nemerteans of the west and northwest coasts of North America. *Bulletin of the Museum at Harvard College*. xlvii:1-318.

5. —. 1940. Revision of the nemertean fauna of the Pacific coasts of north, central and northern South America. Allan Hancock Pacific Expeditions. Reports. 2:247-323.
6. GIBSON, R. 1970. The nutrition of *Paranemertes peregrina* (Rhynchocoela: Hoplonemertea). II. Observations on the structure of the gut and proboscis, site and sequence of digestion, and food reserves. Biological Bulletin. 139:92-106.
7. —. 1972. Nemerteans. Hutchinson, London.
8. HADERLIE, E. C. 1975. Phylum Nemertea (Rhynchocoela), p. 112-120. *In: Light's manual: intertidal invertebrates of the central California coast.* S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
9. —. 1980. Polychaeta: The Marine annelid worms, p. 448-489. *In: Intertidal invertebrates of California.* R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
10. KOZLOFF, E. N. 1974. Keys to the marine unvertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
11. MASLAKOVA, S. A., and J. VON DOHREN. 2009. Larval development with transitory epidermis in *Paranemertes peregrina* and other hoplonemerteans. Biological Bulletin. 216:273-292.
12. ROE, P. 1971. Life history and predator-prey interactions of the Nemertean *Paranemertes peregrina* Coe. Ph.D. University of Washington, Seattle.
13. —. 1976. Life-history and predator-prey interactions of nemertean *Paranemertes peregrina* Coe. Biological Bulletin. 150:80-106.
14. —. 1979. A Comparison of aspects of the biology of *Paranemertes peregrina* (Nemertea) from Bodega Harbor, California, and Washington State. Pacific Science. 33:281-287.
15. ROE, P., J. L. NORENBURG, and S. MASLAKOVA. 2007. Nemertea, p. 221-233. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. T. Carlton (ed.). University of California Press, Berkeley, CA.
16. STRICKER, S. A. 1982. The Morphology of *Paranemertes sanjuanensis* sp-n (Nemertea, Monostilifera) from Washington, USA. Zoologica Scripta. 11:107-115.
17. STRICKER, S. A., and R. A. CLONEY. 1981. The Stylet apparatus of the nemertean *Paranemertes peregrina*: its ultrastructure and role in prey capture. Zoomorphology. 97:205-223.

Updated 2014

Annelida

Abarenicola pacifica

The lugworm, or sand worm

Phylum: Annelida
Class: Polychaeta
Order: Capitellida
Family: Arenicolidae

Description

Size: Individuals often over 10 cm long and 1 cm wide. Present specimen is approximately 4 cm in length (from South Slough of Coos Bay). On the West coast, average length is 15 cm (Ricketts and Calvin 1971).

Color: Head and abdomen orange, body a mixture of yellow, green and brown with parapodial areas and branchiae red (Kozloff 1993).

General Morphology: A sedentary polychaete with worm-like, cylindrical body that tapers at both ends. Conspicuous segmentation, with segments wider than they are long and with no anterior appendages (Ruppert et al. 2004). Individuals can be identified by their green color, bulbous pharynx (Fig. 1), large branchial gills (Fig. 2) and a J-shaped burrow marked at the surface with distinctive coiled fecal castings (Kozloff 1993).

Body: The body of arenicolids can be divided into three regions based on the presence or absence of branchiae.

Anterior: A non-retractile prostomium is without appendages (Blake and Ruff 2007, Fig. 2). Anterior prebranchial region of six setigers without branchiae and with strong setigerous annuli.

Trunk: Posterior to the prebranchial region is a medial branchial region with large branchial gills from setigers seven to 19 (13 pairs). Thoracic epidermis very thick, strongly aerolated (Fauchald 1977).

Posterior: Caudal region is apodous, asetigerous and without appendages. The pygidium tapers gradually to anus, no appendages (Fig. 2).

Parapodia: (Fig. 3) Segments 1–19 with reduced noto- and neuropodia that are reddish and are far from the lateral line. All parapodia are absent in the caudal region.

Setae (chaetae): (Fig. 3) Bundles of notosetae arise from notopodia near branchiae. Short neurosetae extend along

neuropodium. Setae present on segments 1-19 only (Blake and Ruff 2007).

Eyes/Eyespots: None.

Anterior Appendages: None.

Branchiae: Prominent and thickly tufted in branchial region with bunched setae. Hemoglobin makes the branchiae appear bright red (Kozloff 1993).

Burrow/Tube: Firm, mucus impregnated burrows are up to 40 cm long, with typical fecal castings at tail end. Head end of burrow is collapsed as worm continually consumes mud (Healy and Wells 1959). Water is pumped through burrow by pulsating movements of the body (Ruppert et al. 2004).

Pharynx: Thin-walled pharynx is simple and used for continually feeding on sediment. Pharynx described as a large, eversible sack with mucus glands called buccal papillae (Healy and Wells 1959) (Fig. 1).

Genitalia:

Nephridia: Five pairs of nephridia are naked (without hoods) and situated between parapodia on segments 5–9 (Fig. 2). They are sometimes difficult to observe.

Abarenicola specific characters

Esophageal caeca: Dissection is necessary to identify *Abarenicola* species. *Abarenicola pacifica* is distinct in having esophageal caeca comprised of one large anterior pair and 3–6 smaller pairs (Blake and Ruff 2007, Fig. 4).

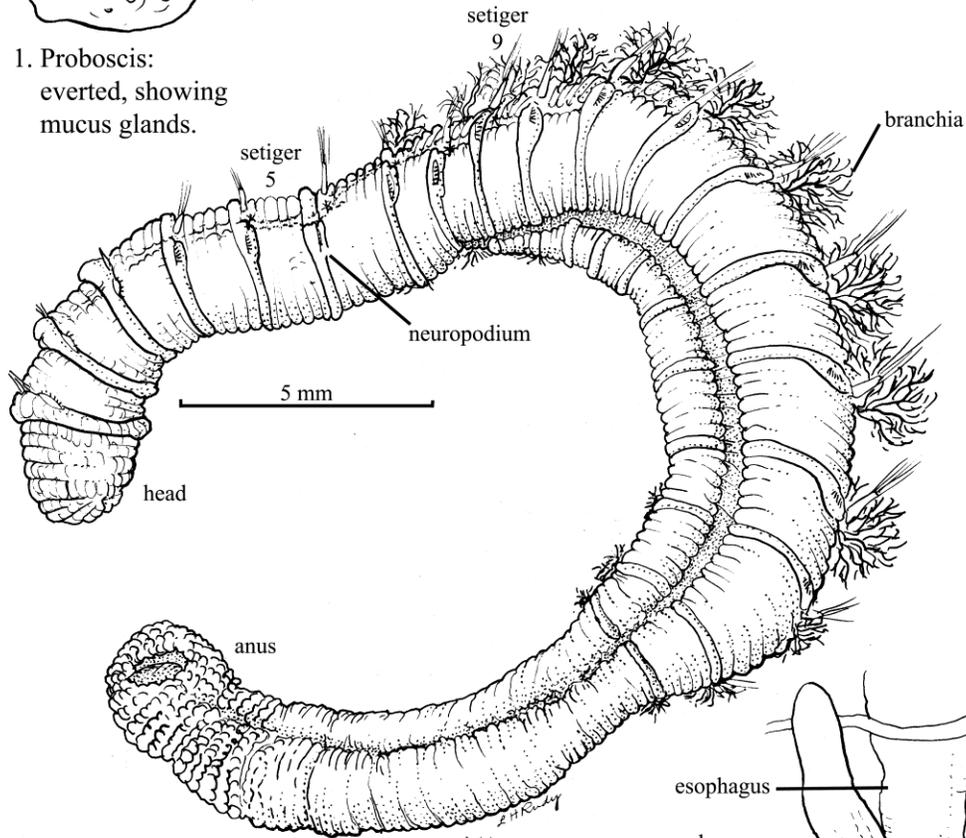
Possible Misidentifications

Other Arenicolidae have the same bushy gills in the middle third of the body. Only the genus *Abarenicola* has well-separated neuropodia, a non-retractile prostomium, more than one pair of esophageal caeca, and five pairs of nephridiopores. Both *Arenicola marina* and *pusilla* have been found in Oregon estuaries. *Abarenicola claparedii oceanica*, has hooded nephridial pores and esophageal caeca composed of 7–9 smaller pairs. *Abarenicola vagabunda*, from Puget Sound (but possibly from Oregon) (Oglesby

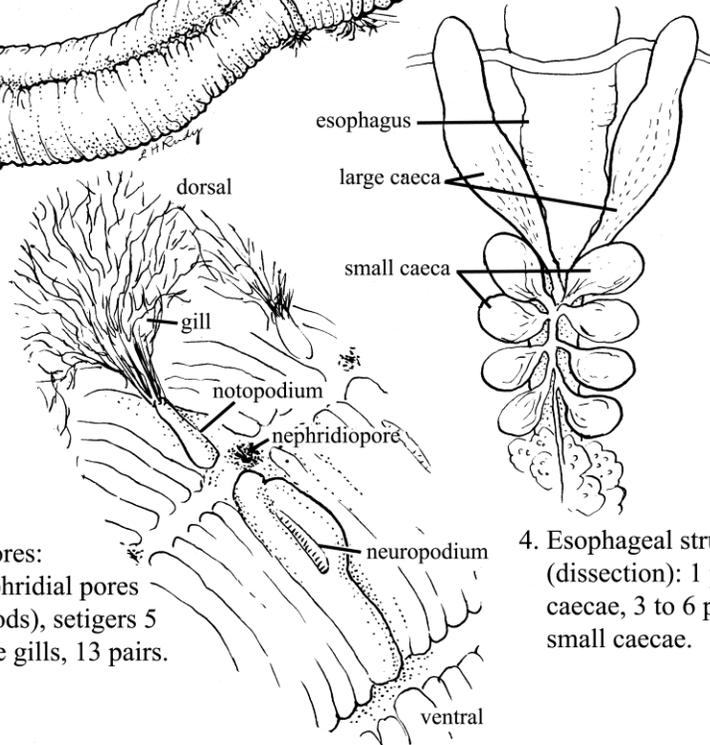
Abarenicola pacifica



1. Proboscis:
everted, showing
mucus glands.



2. *Abarenicola pacifica* x8:
nineteen setigers; orange head,
abdomen; red parapodal areas;
three body sections, medial one
with branchiae.



3. Nephridiopores:
exposed nephridial pores
(without hoods), setigers 5
to 9; fan-like gills, 13 pairs.

4. Esophageal structure
(dissection): 1 pair large
caecae, 3 to 6 pairs
small caecae.

1973), is usually larger and dark brown. It too, has hooded nephridial pores, and smaller esophageal caeca (11–18). Finally, the burrows of *A. vagabunda* are less permanent than *A. pacifica*'s, are found in deep sand and may be more subtidal (Hobson 1966).

Ecological Information

Range: Type locality is Puget Sound (Healy and Wells, 1959). Known range includes Humboldt Bay, California to Alaska, Japan.

Local Distribution: A north Pacific form and the most common lugworm (family Arenicolidae) in Puget Sound area intertidally (Hobson 1966). Found in Coos Bay from estuary mouth to Coos River mouth (marker 15) and at Sunset Bay (Oglesby 1973).

Habitat: Individuals build substantial L- or J-shaped burrows in sand and mud, mixed gravel or mud sediments (South Slough of Coos Bay) (Kozloff 1974). *Abarenicola pacifica* tolerates a muddier, less permeable, more poorly sorted sediment than does *A. c. vagabunda* (Hobson 1966), but does not live in very soft mud (Porch 1970).

Salinity: This species is not found in waters of low salinity or in heavily polluted anaerobic conditions (Porch 1970), but is an osmoconformer and can tolerate a wide range of salinities (lower salinity limit 17.5) (Oglesby 1973).

Temperature: No information is available on temperature tolerance, though temperature fluctuation between 6 and 16° C has been found to significantly affect feeding rate (Hymel and Plante 2000).

Tidal Level: Individuals are common intertidally, but no information on specific tide level is available. Hobson (1967) suggests that distribution is instead based on sediment composition.

Associates: In a commensal relationship, *Pinnixa schmitti* is known to cohabit the burrow of *A. pacifica* (O'Clair and O'Clair 1998).

Abundance: Often to 50/m² (Kozloff 1974) and very dense in specialized habitats. Probably 2nd most abundant macroscopic animal in Coos Bay (Porch 1970). *A. pacifica* was much less abundant than in preceding years-- it was sparse (<1/m²) on Portside beach in April 2015 (Emlet pers com).

Life History Information

Reproduction: Iteroparous. Eggs and sperm discharged from nephridiopores, while both sexes are in their burrows. Males release thin membranous spermatophores (0.5–0.2 mm in diameter) which fall into female burrows and are ruptured by female setae (Okuda 1936; Fernald et al. 1987). Oocytes are pink to pale yellow and 160–190 µm in diameter with conspicuous envelope (Fernald et al. 1987). Fertilization occurs in female's burrow.

Broods are found within burrows January–early April (Washington) and develop within gelatinous masses (Fernald et al. 1987).

Larva: Planktonic larvae are non-feeding and hatch from gelatinous masses within adult tubes as 2 setiger stages (Fernald et al. 1987). Only the larvae of two local Arenicolidae species are known (*Arenicola marina* and *Abarenicola claparedii*, Crumrine 2001).

Juvenile:

Longevity:

Growth Rate: Relative growth rate of 0–6% per day, depending on age and food quality (Linton and Taghon 2000).

Food: Primarily detritus, picked up by mucus of proboscis (Fig. 1) and digested out of sand and mud, which is then defecated.

Depending on sediment type, *A. pacificia* may utilize a variety of feeding modes (deposit, suspension, direct dissolved organic matter uptake) (Hylleberg 1975). Feeding activity by *Abarenicola pacifica* is instrumental in bioturbation and generation of clay laminae (Swinbanks 1981).

Predators: Arenicolids have many predators including most estuarine creatures: man (for fish bait), birds, fish.

Behavior: Most research into the behavior of *A. pacific* is focused on bioturbation and particle selection (Hylleberg 1975).

Bibliography

1. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309–410. *In*: Light and Smith manual: intertidal invertebrates from central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.
2. CRUMRINE, L. 2001. Polychaeta, p. 39–77. *In*: Identification guide to larval marine invertebrates of the Pacific

- Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
3. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. Natural History Museum of Los Angeles County Science Series. 28:1-190.
 4. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In: Reproduction and development of marine invertebrates of the northern Pacific coast.* M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 5. HEALY, E. A., and G. P. WELLS. 1959. Three new lugworms (Arenicolidae, Polychaeta) from the north Pacific area. *Proceedings of the Zoological Society of London.* 133:315-335.
 6. HOBSON, K. D. 1966. Ecological observations on *Abarenicola* species (Polychaeta) of the north Pacific, M. S. University of Washington, Seattle, WA.
 7. HOBSON, K. D. 1967. The feeding and ecology of two North Pacific *Abarenicola* species. (Arenicolidae, Polychaeta). *Biological Bulletin.* 133:323-354.
 8. HYMEL, S. N., and C. J. PLANTE. 2000. Feeding and bacteriolytic responses of the deposit-feeder *Abarenicola pacifica* (Polychaeta : Arenicolidae) to changes in temperature and sediment food concentration. *Marine Biology.* 136:1019-1027.
 9. HYLLEBERG, J. 1975. Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola* and a concept of gardening in lugworms. *Ophelia.* 14:113-137.
 10. KOZLOFF, E. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
 11. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
 12. LINTON, D. L., and G. L. TAGHON. 2000. Feeding, growth, and fecundity of *Abarenicola pacifica* in relation to sediment organic concentration. *Journal of Experimental Marine Biology and Ecology.* 254:85-107.
 13. O'CLAIR, R. M., and C. E. O'CLAIR. 1998. Southeast Alaska's rocky shores: animals. Plant Press, Auke Bay, AK.
 14. OGLESBY, L. C. 1973. Salt and water balance in lugworms (Polychaeta: Arenicolidae), with particular reference to *Abarenicola pacifica* in Coos Bay, Oregon. *Biological Bulletin.* 145:180-199.
 15. OKUDA, S. 1938. Notes on the spawning habits of *Abarenicola claparedii* Levinsen. *Annotationes Zoologicae Japonenses.* 17:577.
 16. PORCH, L. L. 1970. Polychaetes of Coos Bay. *In: OIMB Unpublished Student Report, Summer 1970.*
 17. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides.* Stanford University Press, Stanford, California.
 18. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach.* Thomson Brooks/Cole, Belmont, CA.
 19. SWINBANKS, D. D. 1981. Sediment reworking and the biogenic formation of clay laminae by *Abarenicola pacifica*. *Journal of Sedimentary Petrology.* 51(4): 1137-1145.

Updated 2014
T.C. Hiebert and K. Meyer

Capitella spp. (*Capitella capitata* species complex)

A thread worm

Phylum: Annelida
Class: Polychaeta
Order: Capitellida
Family: Capitellidae

Taxonomy: Once considered a cosmopolitan species, *Capitella capitata* (Fabricius, 1780) is now regarded as a complex of several closely related, morphologically similar but genetically distinct sister species (Grassle and Grassle 1976; Blake 2000; Blake and Ruff 2007). Currently, this species complex consists of at least 6 and as many as 13 species (Blake 2000; Blake et al. 2009), some of which are recognizable by subtle differences in morphology (Grassle and Grassle 1976) or reproductive ecology. *Capitella telata* was recently described (Blake et al. 2009). Teasing apart sister species based on morphology is difficult and most researchers refer, instead, to the entire complex of species (e.g. *Capitella capitata sensu lato*, Blake and Ruff 2007).

Description

Size: Individuals range from 20–100 mm in length and 1–2 mm in width, with at least 90 segments (Blake 2000).

Color: Dark red or brownish, fixed specimens are light tan.

General Morphology: Long and earthworm-like with pointed anterior (Hartman and Reish 1950; Hartman 1969; family Capitellidae, Blake and Ruff 2007). Body cylindrical, slender and without obvious parapodia or peristomial appendages.

Body: Body divided into anterior thoracic and posterior abdominal regions. (Fig. 1: drawing done from somewhat compressed specimen). Circulatory system lacking (Morris et al. 1980).

Anterior: Broad and triangular prostomium with dorsal depression (Hartman 1969; Blake 2000) (Fig. 2). Prostomium shape variable between species (sharply pointed, conical or swollen) (Blake 2000). Peristomium short and setigerous.

Trunk: Anterior thorax with nine segments, all bearing setae.

Abdomen of 90 segments beginning at setiger 10.

Posterior: Pygidium is a simple posterior flange (Hartman 1969) without appendages (Blake 2000).

Parapodia: Biramous and inconspicuous (Hartman 1944). Parapodia reduced in thoracic region becoming swollen in abdominal segments (Blake 2000). Notopodia become elevated posteriorly in posterior abdominal region (Blake 2000).

Setae (chaetae): Simple (not jointed). Anterior thoracic parapodia (setigers 1–7) with long, fine capillary spines (Fig. 5a). Abdominal segments with stout hooks and transparent hoods (Fig. 5b). Hooks composed of a large main fang with a straight row of apical teeth where each tooth is well separated. Tooth number varies with 1–3 rows of 1–5 teeth per row (Blake 2000). Eighth and ninth neuropodia each with two stout yellow copulatory spines (male, Fig. 4a).

Eyes/Eyespots: None in described specimen. Although some members of the species complex may possess small, paired eyespots (Blake 2000).

Anterior Appendages: None.

Branchiae: None.

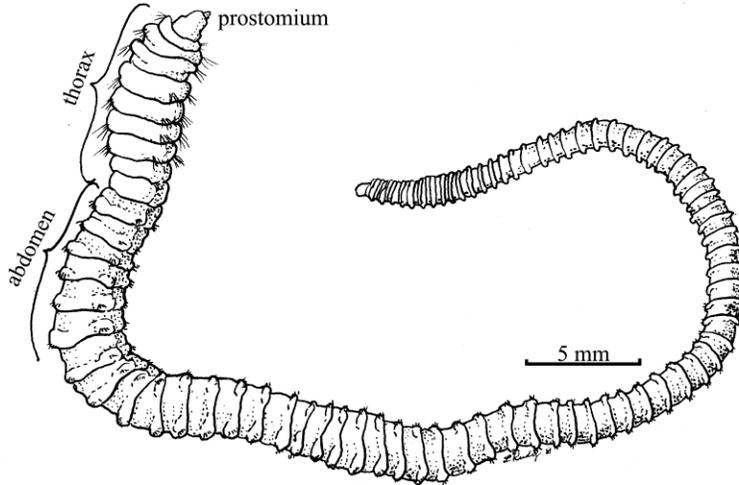
Burrow/Tube: Individuals inhabit black membranous, mucus-lined burrows in fine mud and organic sediments (Fernald et al. 1987). Within the vertically positioned tube, individuals are situated such that their head is up (Ricketts and Calvin 1952).

Pharynx: Bears eversible proboscis which is rarely seen everted (Hartman 1969).

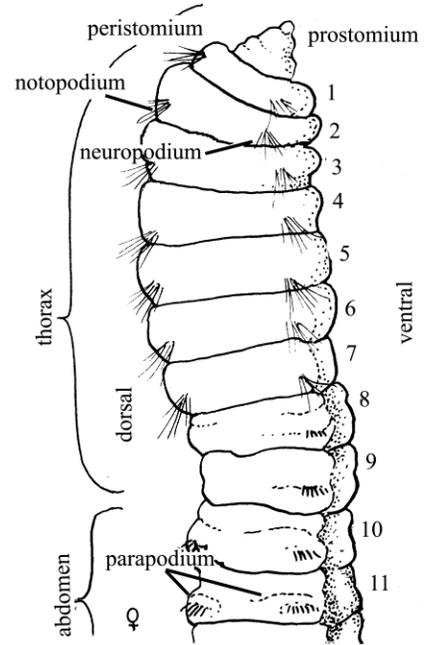
Genitalia: Males with lateral generative pore between setigers 7 and 8 and 2 yellow genital spines in each notopodium of setigers eight and nine. Notopodial spines number six or more on setiger eight and 2–4 on setiger nine (Blake 2000). Females with corresponding genital pores (Blake 2000).

Nephridia:

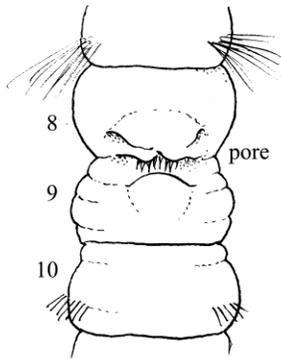
Capitella sp.
(*Capitella capitata*)



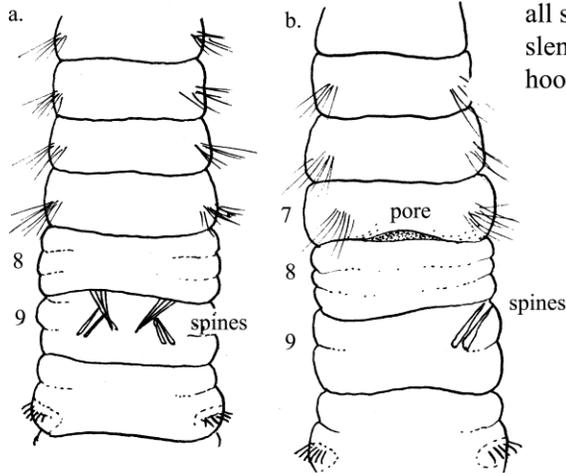
1. *Capitella sp.* (lateral view) ♀ x4:
dark red body, threadlike, with 9 thoracic and about 90 abdominal setigers; prostomium a depressed triangular lobe, without eyes or appendages.



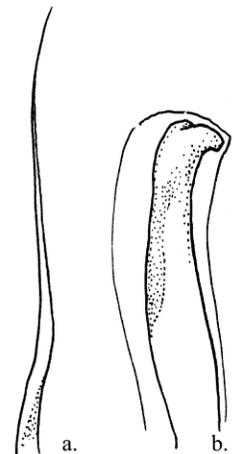
2. Prostomium and anterior setigers (lateral view) x30:
setae begin on peristomium; biramous parapodia, no branchiae; all setae simple, thoracic long, slender; abdominal stout, hooded hooks.



3. Female genital area (dorsal view): showing genital pore between setigers 8 and 9.



4. Male genital area:
a. (dorsal view) showing two copulatory spines on each notopodium, setigers 8 and 9.
b. (lateral view) generative pore between setigers 7 and 8.



5. Setae:
a. long, fine capillary seta (thorax).
b. stout, hooded hook (abdomen).

Possible Misidentifications

The Capitellidae lack conspicuous parapodia, branchiae, lobes and prostomial appendages. Their superficial appearance is earthworm-like. Capitellid genera are defined by characters (e.g. numbers of thoracic setigers with and without capillary setae and the first appearance of hooks) which are ontogenically dependent (Blake 2000). Identification requires adult specimens as the same species could be identified to two different genera at different developmental stages (Fredette 1982). Several genera occur locally in muddy estuarine situations:

Heteromastus spp. have 12 thoracic segments (not 11) and one is achaetous. Capillary setae are present on the first five setigers. Uncini begin on setiger six (not five) and they have notopodial branchiae on distal posterior segments.

Notomastus spp. like *Heteromastus*, have 12 thoracic segments (not 11) and one is achaetous. Some species possess branchiae. All thoracic setigers have capillary setae (as in Fig. 5).

Mediomastus spp. have an elongated, pointed prostomium and thorax with achaetous peristomium and 10 setigers (not nine). Capillary setae are present on setigers 1–4 (not 1–7) and long-handled hooks are present on setigers 5–10.

Capitella spp. are differentiable from the other genera by the presence of hooks as well as capillary setae on the last two thoracic setigers (Hartman 1969) as well as genital spines on setigers eight and nine. Members of the *Capitella capitata* species complex are the only members of this genus to possess setae on the first segment (Hartman and Reish 1950) (Fig. 2).

Ecological Information

Range: Type locality is Naples. Chiefly northern distribution including western Canada to California (Hartman 1969). Cosmopolitan. Many species have wide and overlapping distribution (Blake 2000).

Local Distribution: In Coos Bay stations include South Slough, North Spit and Barview. Also Netarts Bay at several stations (Stout 1976).

Habitat: Mudflats, muddy sand to pure mud (Porch 1970), can be found in fish wastes,

sulfurous sediments and organically enriched sediments where it may be a pollution indicator if found in great numbers and in the absence of many other invertebrate species (Filice 1959; Reish 1955). This does not hold true in Coos Bay, where it is not found in the polluted areas (Porch 1970). Found in vertical, dirt-encrusted, black, membranous tubes (Ricketts and Calvin 1971), in the mud of *Salicornia* marsh channels, Coos Bay (Porch 1970). No real preference for substrate, but likes quite intertidal conditions (Filice 1959).

Salinity: Can tolerate low saline condition (Porch 1970), collected at salinity of 14, San Francisco Bay where it is reported to prefer saline conditions (Filice 1959).

Temperature: Cold waters to tropics, more commonly in temperate waters (Morris et al. 1980).

Tidal Level: Collected at +0.9 m to -1.2 m, particular about depth, not substrate. Also found down to approximately 55 m (Filice 1959).

Associates: Coos Bay associates include other polychaetes: *Abarenicola*, *Mediomastus* (Netarts Bay), *Leptochelia*, *Pinnixa* and amphipods (Morris et al. 1980).

Abundance: Common, cosmopolitan in mudflats (Blake 1975). When present in great numbers in an area with few other invertebrates, heavy pollution of the habitat may be indicated (Reish 1955). Found in great beds of many acres on the Berkeley, California mudflats (Ricketts and Calvin 1971).

Life-History Information

Reproduction: Great variability exists within this complex of species from sexually dimorphic to hermaphroditic species (George 1984 in Blake 2000). Special copulatory setae on setigers eight and nine (Fig. 4). Reproductively active all year (California) with mild peaks summer and winter. Males transfer spermatophores to females which can store them until eggs are ripe. Early development occurs in the female's tube. Developmental modes also vary from direct or lecithotrophic development of short duration (e.g. hours) to planktotrophic development with short pelagic duration (weeks) (Crumrine 2001). Egg diameters correspond to

developmental mode and range from 50–250 µm (Grassle and Grassle 1976).

Larva: Larvae emerge from female tube after five days as trochophore larvae or hatch at 7–14 days as juveniles. Trochophore larvae have reduced or absent apical tuft, prototroch and telotroch, with gut that is not subdivided (Crumrine 2001). Metatrochophores settle to the benthos (Blake 2000) and settlement may be stimulated by an increase in hydrogen sulfide (Cuomo 1985 in Fernald et al. 1987).

Juvenile:

Longevity: Juveniles reach sexual maturity rapidly, within one month at 20° C.

Growth Rate: Members of this species complex have rapid life-cycles and rearing several generations in the laboratory is relatively straightforward (Fernald et al. 1987).

Food: A direct deposit feeder on organic matter and indicator of polluted sediments.

Predators:

Behavior:

Bibliography

1. BLAKE, J. A. 1975. Phylum Annelida: Class Polychaeta, p. 151-243. *In:* Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
2. —. 2000. Family Oweniidae, p. 97-127. *In:* Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel. Vol. 7. J. A. Blake, B. Hilbig, and P. V. Scotts (eds.). Santa Babara Museum of Natural History, Santa Babara, California.
3. BLAKE, J. A., J. P. GRASSLE, and K. J. ECKELBARGER. 2009. *Capitella teleta*, a new species designation for the opportunistic and experimental *Capitella* sp. I, with a review of the literature for confirmed records. *Zoosymposia*. 2:25-53.
4. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In:* Light and Smith manual: intertidal invertebrates from central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.
5. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In:* Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
6. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In:* Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
7. FILICE, F. P. 1959. The effect of wastes on the distribution of bottom invertebrates in the San Francisco Bay estuary. *Wasmann Journal of Biology*. 17:1-17.
8. FREDETTE, T. 1982. Evidence of ontogenetic setal changes in *Heteromastus filiformis* (Polychaeta: Capitellidae). *Proceedings of the Biological Society of Washington*. 95:194-197.
9. GRASSLE, J. P., and J. F. GRASSLE. 1976. Sibling species in the marine pollution indicator *Capitella* (Polychaeta). *Science*. 192:567-569.
10. HARTMAN, O. 1944. Polychaetous annelids. Parts V-VIII. Allan Hancock Foundation of Scientific Research. Allan Hancock Pacific Expeditions. Reports. 10:1-525.
11. —. 1969. Atlas of the Sedentariate Polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
12. HARTMAN, O., and D. J. REISH. 1950. The marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
13. MORRIS, R. H., D. P. ABBOTT, and E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford.
14. PORCH, L. L. 1970. Polychaetes of Coos Bay. *In:* OIMB Unpublished Student Report, Summer 1970.
15. REISH, D. J. 1955. The relation of the polychaetous annelids to harbor pollution. *U.S. Public Health Reports*. 70:1168-1174.

16. RICKETTS, E. F. 1952. Between Pacific tides. Stanford: Stanford University Press, Stanford.
17. RICKETTS, E. F., and J. CALVIN. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
18. STOUT, H., and S. V. SHABICA. 1976. The natural resources and human utilization of Netarts Bay, Oregon. Oregon State University, Corvallis, Oregon.

Updated 2014

Mediomastus californiensis

A mud dwelling thread worm

Phylum: Annelida
Class: Polychaeta
Order: Capitellida
Family: Capitellidae

Description

Size: Individuals range from 25–35 mm in length, are less than 1 mm in width and have 100 segments (Hartman 1969). Specimens from Coos Bay have 60–120 segments.

Color: Translucent (Hartman 1969), light tan to colorless (fixed, Blake 2000). Specimens from Coos Bay are reddish brown.

General Morphology: Long and thread-like (Hartman 1969), resembling an earthworm with pointed anterior (family Capitellidae, Blake and Ruff 2007).

Body: Body divided into anterior thoracic and posterior abdominal regions. Widest at thoracic setigers two and three and at anterior abdominal segments. Segments annulate, with ridges (Fig. 2) and short anteriorly becoming longer and cylindrical posteriorly. Change from thorax to abdomen indistinct where texture of thorax is wrinkled and abdomen is smooth.

Anterior: Prostomium small and conical with short palpode at anterior end, followed by a depressed ring (often lost in collecting, Fig. 2).

Trunk: Thoracic region is wrinkled in texture and includes segments 1–11 (= setigers 1–10) which are biannulate (genus *Mediomastus*, Hartman 1944) (Fig. 2). The first segment is achaetous and longer than following setiger (setiger 1). Thoracic setigers bear both simple capillary setae (setigers 1–4) and hooded hooks (= uncini, setigers 5–10) and segments bearing capillary setae are shorter than those with hooks (Blake 1975, 2000). Abdominal segments are smooth and coiled with first segment (=setiger 11) shorter than following (Hartman 1944). Abdominal setigers bear hooded hooks only, which vary in number anteriorly and posteriorly (Blake 2000). Most posterior segments become short again, have more elevated parapodia but are not conspicuous. Many Coos Bay

specimens with short, bell-shaped posterior segments (Fig. 3).

Posterior: Pygidium with single cirrus attached ventrally and easily lost in collecting (Fig. 4).

Parapodia: Biramous and inconspicuous (Hartman 1944). Thoracic parapodia more developed than abdominal (Blake 2000).

Setae (chaetae): Simple and unjointed consisting of capillary setae (setigers 1–4) and long handled hooded hooks (=uncini, setigers five and on). Thoracic capillaries limbate and abdominal capillaries absent. Thoracic notosetae with 5–15 setae per fascicle, neurosetae with 5–11 setae per fascicle. Thoracic notopodial uncini with 4–8 hooks per fascicle and neuropodial uncini with 5–10 hooks per fascicle. Anterior abdominal notopodia bear 5–7 uncini with posterior region reduced to two hooks per fascicle while neuropodial anterior abdominal uncini have 8–10 uncini which are reduced posteriorly to four hooks per fascicle (Blake 2000) (Fig. 2, 5). Abdominal uncini with shorter hoods than thoracic (Blake 2000) and uncini on segments 10–11 are dorsolateral but not modified for copulation (Hartman 1944). Each uncini bears a large fang with 3–12 apical teeth in 1–3 rows.

Eyes/Eyespots: Two small eyes, mid-dorsally on prostomium (Blake 2000).

Anterior Appendages: None (family Capitellidae, Fauchald 1977).

Branchiae: None.

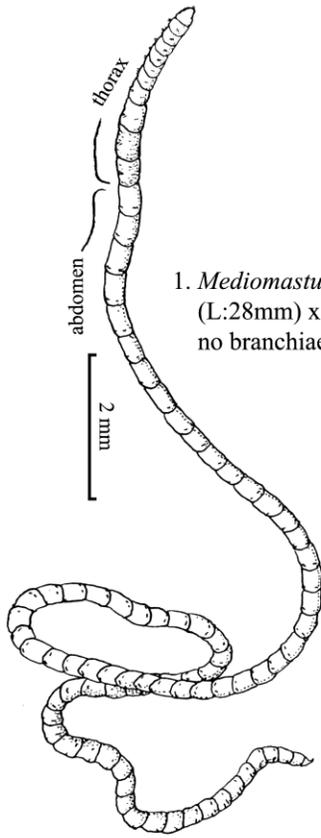
Burrow/Tube: In soft often anoxic sediments and near the surface to 15 cm depth (family Capitellidae, Blake 2000).

Pharynx: Bears proboscis with is a soft, papillose, glandular sac with tiny widely scattered low papillae (Hartman 1944) (Fig. 2) are sometimes dense in distribution (Blake 2000).

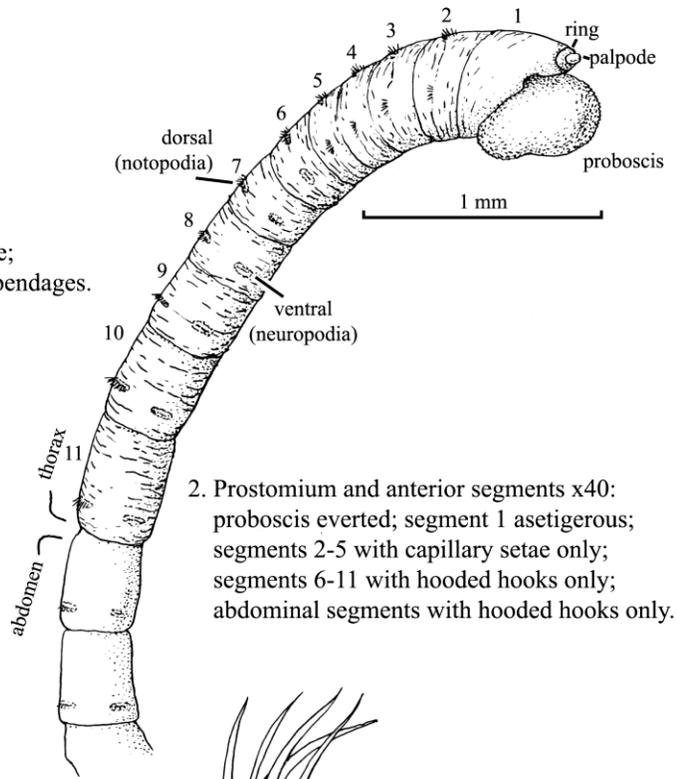
Genitalia: No thoracic genital spines.

Nephridia: Nephridiopores present between setigers 5–6, 7–8, 8–9, 9–10 (Blake 2000).

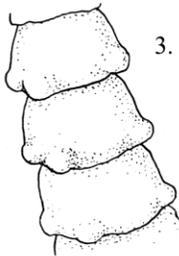
Mediomastus californiensis



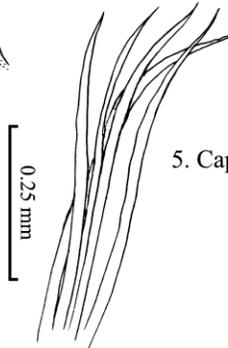
1. *Mediomastus californiensis* (L:28mm) x12: earthworm-like; no branchiae or prostomial appendages.



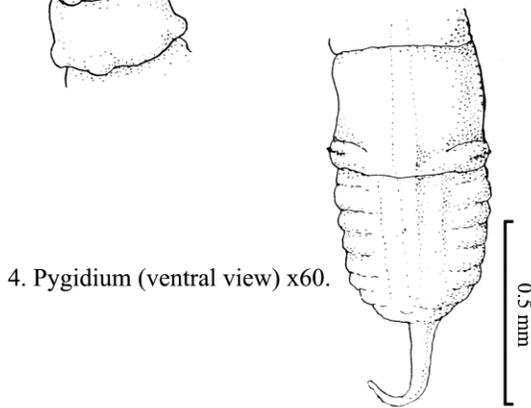
2. Prostomium and anterior segments x40: proboscis everted; segment 1 asetigerous; segments 2-5 with capillary setae only; segments 6-11 with hooded hooks only; abdominal segments with hooded hooks only.



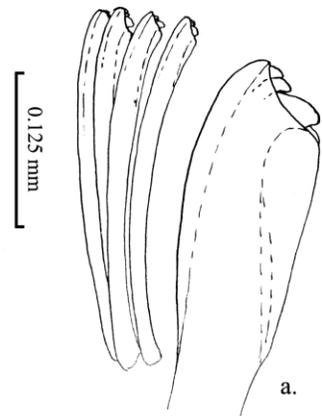
3. Some posterior segments x60.



5. Capillary setae x100.



4. Pygidium (ventral view) x60.



6. Hooded hooks (uncini) x200: a. enlargement x800.

Possible Misidentifications

The Capitellidae lack conspicuous parapodia, branchiae, lobes and prostomial appendages. Their superficial appearance is earthworm-like. Capitellid genera are defined by characters, which are ontogenically dependent (e.g. numbers of thoracic setigers with and without capillary setae and the first appearance of hooks (Blake 2000). Identification requires adult specimens because the same species could be identified to two different genera at different developmental stages (Fredette 1982). Several genera occur locally in muddy estuarine situations:

Capitella spp. have hooks as well as capillary spines on the thoracic setigers but lack an achaetous first segment. They have large genital spines on segments eight and nine and all nine thoracic segments bear setae.

Heteromastus spp. have 12 thoracic segments (not 11) and one is achaetous. Uncini begin on setiger six (not five) and they have notopodial branchiae on distal posterior segments.

Notomastus spp. like *Heteromastus*, have 12 thoracic segments (not 11) and one is achaetous. Some species possess branchiae. All thoracic setigers have capillary setae (as in Fig. 5).

Three species in the genus *Mediomastus* occur locally (including *M. californiensis*, Blake and Ruff 2007).

Mediomastus acutus occurs in fine silty mud in the shallow subtidal (Blake and Ruff 2007) has a long pointed prostomium and limbate as well as paddle-like thoracic capillaries (Warren et al. 1994). This very thin species, only about 9 mm in length, has been found in Coos Bay (H. Jones pers. com.) and off southern California (Hartman 1969).

Mediomastus ambiseta co-occurs with *M. californiensis* (Blake 2000). *M. californiensis* can be differentiated from *M. ambiseta* by its large size, similarity of thoracic and abdominal hooks (which are dimorphic in *M. ambiseta*), lack of abdominal capillaries or spine-like hooks (Blake 2000). *Mediomastus ambiseta* also has posterior notopodia with 1–2 capillary setae and has been found subtidally in Washington (Hobson and Banse 1981).

(see Warren et al. 1994 for differentiating *Mediomastus* species).

Ecological Information

Range: NE Pacific distribution includes the Aleutian Islands and Alaska (H. Jones pers. com.), British Columbia, Washington, Oregon, California and Gulf of Mexico (Blake 2000). Also along Atlantic coast in Florida (Santos and Simon 1980), New England to Chesapeake Bay (Blake 2000).

Local Distribution: Coos Bay intertidal. Also Yaquina Bay.

Habitat: Compact, fine muddy sand (Hartman 1947).

Salinity: Found in salinities of 30.

Temperature:

Tidal Level: At low water line (Hartman 1947) and intertidal to shelf depths (Blake and Ruff 2007).

Associates: *Capitella* sp. *capitata* in Coos Bay and *Notomastus tenuis* in Tomales Bay, California (Hartman 1944).

Abundance: A Coos Bay (South Slough) core (13cm height x 15 cm diameter) at high tide (=1.10 m) yielded one specimen, at mid tide (=1.04 m) up to five specimens and at low tide (=0.90 m) up to 10 specimens (Posey 1985). 5000 individuals/m have been reported in Massachusetts Bay, MA (Blake et al. 1987).

Life-History Information

Reproduction: Oocyte diameter approximately 60 μm (Warren et al. 1994). Gametes were observed in *M. ambiseta* where oocytes were 75 μm (Grassle and Grassle 1985 in Blake 2000).

Larva: Development is highly variable among capitellids and *M. californiensis* larvae have not been described. The larvae of *M. fragile* hatch from egg masses after 3–4 days and develop as planktotrophic trochophore larvae (Hansen 1993). Artificially fertilized *M. ambiseta* embryos were swimming trochophore larvae after three days, were metatrochophores by eight days and settled at 13 days when larvae were 13-setiger stage (Grassle and Grassle 1985 in Blake 2000).

Juvenile:

Longevity: *Mediomastus ambiseta* juveniles were sexually mature after 74 days (Grassle and Grassle 1985 in Blake 2000).

Growth Rate: An "R-strategist", *M. californiensis* can attain a large population rapidly (e.g. Florida, Santos and Simon 1980).

Food: A direct deposit feeder.

Predators:

Behavior:

Bibliography

1. BLAKE, J. A. 1975. Phylum Annelida: Class Polychaeta, p. 151-243. *In*: Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
2. —. 2000. Family Capitellidae, p. 47-96. *In*: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
3. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
4. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. Natural History Museum of Los Angeles County Science Series. 28:1-190.
5. FREDETTE, T. J. 1982. Evidence of ontogenetic setal changes in *Heteromastus filiformis* (Polychaeta: Capitellidae). Proceedings of the Biological Society of Washington. 95:194-197.
6. HANSEN, B. 1993. Aspects of feeding, growth and stage development by trochophora larvae of the boreal polychaete *Mediomastus fragile* (Rasmussun) (Capitellidae). Journal of Experimental Marine Biology and Ecology. 166:273-288.
7. HARTMAN, O. 1944. Polychaetous annelids from California: including the descriptions of two new genera and nine new species. University of Southern California Press, Los Angeles.
8. —. 1947. Polychaetous annelids. Allan Hancock Pacific Expeditions. Reports. 10:391-481.
9. —. 1969. Atlas of the Sedentariate Polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
10. HOBSON, K. D., and K. BANSE. 1981. Sedentariate and archiannelid polychaetes of British Columbia and Washington. Canadian Bulletin of Fisheries and Aquatic Sciences. 209:1-144.
11. POSEY, M. H. 1985. The effects upon the macrofaunal community of a dominant burrowing feeder, *Callianassa californiensis*, and the role of predation in determining its intertidal distribution. Ph.D. University of Oregon.
12. SANTOS, S. L., and J. L. SIMON. 1980. Response of soft-bottom benthos to annual catastrophic disturbance in a South Florida estuary. Marine Ecology Progress Series. 3:347-355.
13. WARREN, L. M., P. A. HUTCHINGS, and S. DOYLE. 1994. A revision of the genus *Mediomastus* Hartman, 1944 (Polychaeta: Capitellidae). Records of the Australian Museum. 46:227-256.

Updated 2014

Armandia brevis

Phylum: Annelida
Class: Polychaeta
Order: Opheliida
Family: Opheliidae

Taxonomy: *Armandia bioculata* (Hartman 1948), once thought to be a separate species, was synonymised with *A. brevis* in 1975 (Blake).

Description

Size: Individuals 7–25 mm in length and 1–1.5 mm in width (Hermans 1977). The illustrated specimen is 1–2 cm in length (Fig. 1).

Color: Pale flesh color to orange red, rather transparent.

General Morphology: With 29–30 segments, body slender and somewhat stiff (personal communication, R. Boomer) and tapers dramatically at anterior and posterior.

Body: Recognizable by a ventral groove, sleek body and lateral eyespots.

Anterior: Prostomium cone-shaped and sharply pointed, with small terminal palpode, nuchal organs (Fig. 3) and three prostomial eyes (Hermans 1977).

Trunk: A distinct ventral groove runs the entire body length (Fig. 1).

Posterior: Pygidium elongated and pointed with a long and unpaired cirrus and eight short papillae (Blake and Ruff 2007) (Fig. 4).

Parapodia: Small biramous parapodia are present on 29 setigers (Blake and Ruff 2007).

Setae (chaetae): Bundles of chaetae on noto- and neuropodia are simple and colorless (Hermans 1977). Notosetae are twice as long as neurosetae.

Eyes/Eyespots: Three eyes on prostomium (Hermans 1977). Eleven pairs of dark eyespots exist laterally on body segments 7–17. They are dark, paired and located near the branchiae (Fig. 2).

Anterior Appendages: Anterior feeding palps present (Fig. 3).

Branchiae: Present from the second segment posterior, cirriform (1 mm in length)

and simple. Branchiae curl dorsally (Hermans 1977).

Burrow/Tube: *Armandia brevis* is an active burrower and does not inhabit a permanent burrow.

Pharynx: Proboscis is used to ingest particle and is slipper-shaped and tongue-like (Hermans 1977).

Genitalia: Small slits that only open when spawning (Hermans 1977).

Nephridia: Eleven pairs in segments 14–24, nephridiopores lacking (Hermans 1977).

Possible Misidentifications

Among the Opheliidae, there are at least six genera in our area, all of which are sand or mud dwellers with limited segmentation, simple prostomia, biramous parapodia and capillary setae.

Thoracophelia (= *Euzonus*) spp. live on clean sandy beaches and have three distinct body regions: an inflated anterior set off from the thoracic region with a marked constriction and a narrow posterior with branchiae and a ventral groove.

Ophelina (= *Ammotrypane*) spp. have a ventral groove along the whole body length (Fauchald 1977), cirriform branchiae only on posterior setigers, no lateral eyes and a long narrow anal tube with two internally attached ventral cirri (ibid).

Travisia spp. are cigar-shaped, without a ventral groove but with branchiae and their posterior parapodia have large lobes.

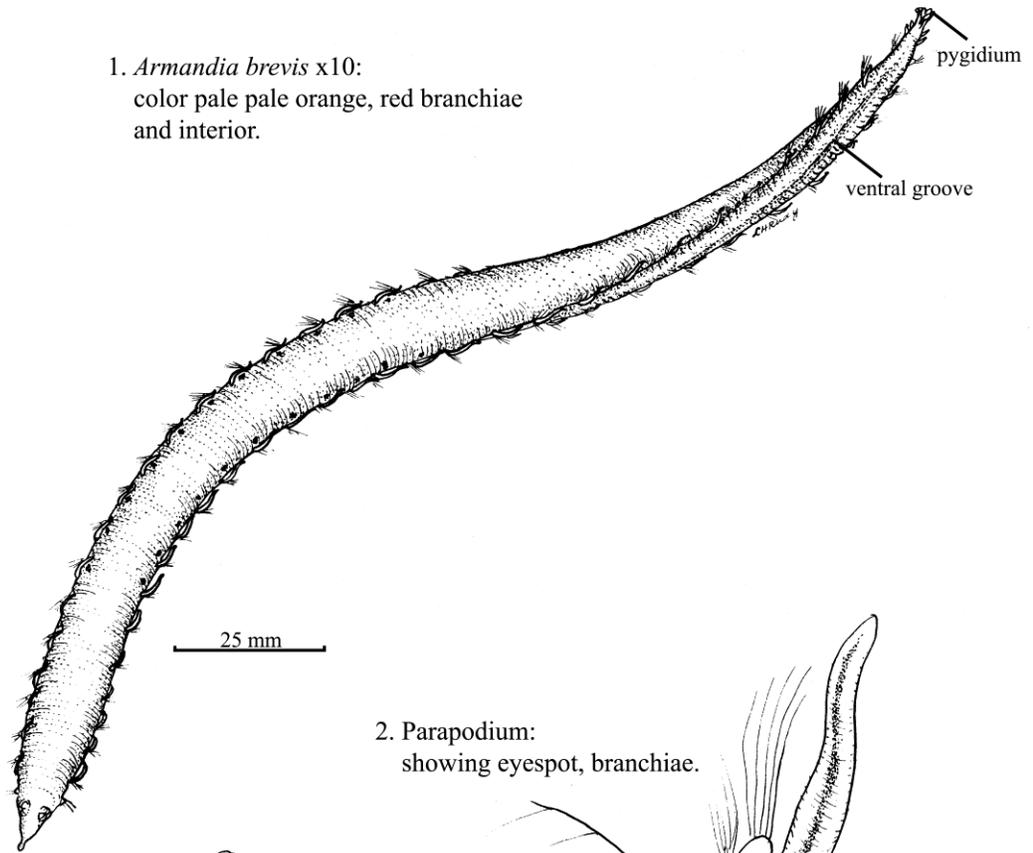
Polyophthalmus spp. have a ventral groove along the whole body length, no branchiae but lateral eyes. They have a short anal tube with small anal cirri (Fauchald 1977).

Ophelia spp. have a fusiform body morphology, inflated anterior and posterior ventral groove. They generally have branchiae on setigers 8–10.

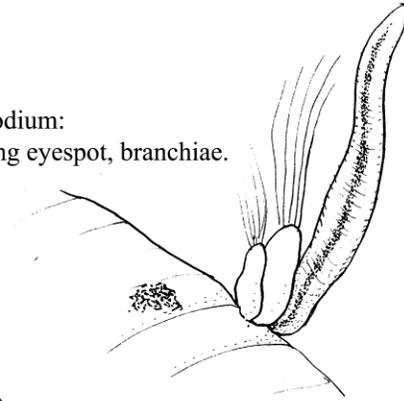
Armandia spp. can be differentiated from other genera by a ventral groove along

Armandia brevis

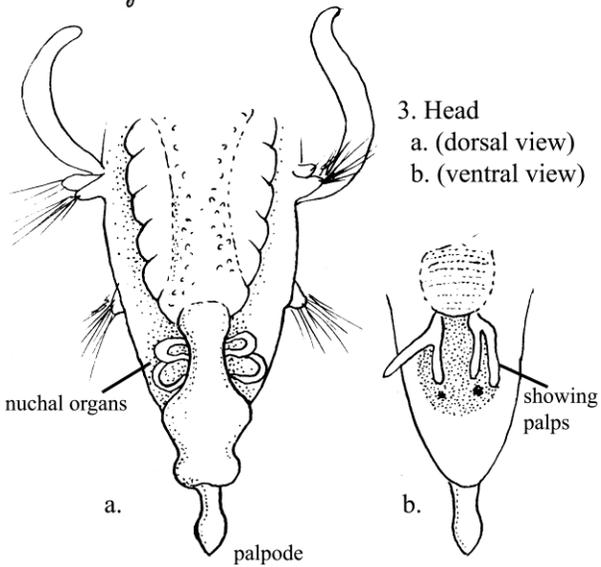
1. *Armandia brevis* x10:
color pale pale orange, red branchiae
and interior.



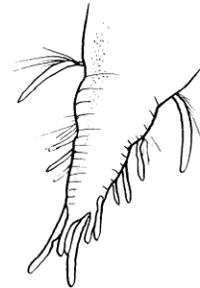
2. Parapodium:
showing eyespot, branchiae.



3. Head
a. (dorsal view)
b. (ventral view)



4. Pygidium (dorsal view):
with long cirri.



the whole body length, cirriform branchiae, lateral eyes and a long slender anal tube with paired long and internally attached ventral cirri and shorter dorsal cirri. *Armandia brevis* is the only local species in the genus *Armandia*.

Ecological Information

Range: Type locality is Alaska and the known range now extends to California.

Local Distribution: Found in South Slough of Coos Bay and at Cape Arago (Hartman and Reish 1950).

Habitat: Sandy mud (e.g. Metcalf Preserve on South Slough) and loose sand (Ricketts and Calvin 1971).

Salinity:

Temperature:

Tidal Level: Shore to 73 m in Alaska and +0.36 m in Coos Bay (South Slough) and Puget Sound (Woodin 1974).

Associates: *Pista pacifica* and other small polychaetes as well as the amphipod *Corophium brevis*.

Abundance: 720/m (Hartman 1944) in Mitchell Bay (San Juan Islands, WA) (Woodin 1974).

Life-History Information

Reproduction: Ripe epitokous individuals free spawn gametes at night in April–November (WA, Woodin 1974; Hermans 1977) which are fertilized in the water column. Newly fertilized eggs are spherical and 50 μm in diameter, undergo classic spiral cleavage and become swimming blastulae after 12 hours (11–13°C, Hermans 1977).

Larva: Planktotrophic trochophore larvae develop in less than two days and are competent to metamorphose after 3–7 weeks (20 segments, Hermans 1977). See Hermans 1977 for description of larval development and metamorphosis.

Juvenile: Growth is rapid where nine segments are added and reproduction begins six weeks post settlement (Fernald et al. 1987).

Longevity: Individuals reach sexual maturity at six weeks at which point they spawn and die (Hermans 1977; Fernald et al. 1987).

Growth Rate: Up to 2–3 generations per summer (Hermans 1966).

Food: A deposit feeder (Hermans 1966), ingesting sediment while burrowing with an eversible pharynx (Ruppert et al. 2004).

Predators: *Cancer magister*.

Behavior: As is true for other members of the Opheliidae, *A. brevis* is an active and rapid burrower, usually within 3 cm of the surface, a behavior which aids in escape from predators. Individuals can swim through loose sand as rapidly as some worms are able to swim in water (MacGinitie 1935 in Ricketts and Calvin 1952).

Bibliography

1. BLAKE, J. A. 1975. Phylum Annelida: Class Polychaeta, p. 151-243. *In:* Light's Manual: Intertidal Invertebrates of the Central California Coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
2. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In:* Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.
3. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. Natural History Museum of Los Angeles County Science Series. 28:1-190.
4. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In:* Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
5. HARTMAN, O. 1944. Polychaetous annelids from California, including the descriptions of two new genera and nine new species. A. Hancock Pacific Expedition. 10:239-310, p. 284-5.
6. —. 1948. The Polychaetous annelids of Alaska. Pacific Science. 2:3-58.
7. HARTMAN, O., and D. J. REISH. 1950. The Marine Annelids of Oregon. Oregon State College, Corvallis, Oregon.

8. HERMANS, C. O. 1966. The Natural History and Larval Anatomy of *Armandia brevis* (Polychaeta: Opheliidae), p. 175. Vol. Ph.D. University of Washington, Seattle, WA.
9. —. 1977. Metamorphosis in the Opheliid polychaete *Armandia brevis*, p. 113-126. *In: Settlement and Metamorphosis of Marine Invertebrate Larvae*. R. Chia and M. E. Rice (eds.). Elsevier, New York.
10. RICKETTS, E. F. 1952. Between Pacific Tides: An Account of the Habits and Habitats of Some Five Hundred of the Common, Conspicuous Seashore Invertebrates of the Pacific Coast Between Sitka, Alaska, and Northern Mexico. Stanford University Press, Stanford, CA.
11. RICKETTS, E. F., and J. CALVIN. 1971. Between Pacific Tides. Stanford University Press, Stanford, CA.
12. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. Invertebrate Zoology: A Functional Evolutionary Approach. Thomson Brooks/Cole, Belmont, CA.
13. WOODIN, S. A. 1974. Polychaete abundance patterns in a marine soft-sediments environment: The importance of biological interactions. *Ecological Monographs*. 44:171-187.

Updated 2014

Ophelia assimilis

A sand worm

Phylum: Annelida
Class: Polychaeta
Order: Opheliida
Family: Opheliidae

Description

Size: Individuals up to 33 mm in length and 4 mm in width (Hartman 1969). The described specimen (Fig. 1) was 22 mm in length.

Color: Specimens collected in Coos Bay are white or pink iridescent.

General Morphology: Fusiform (cigar-shaped) and weakly segmented, with 33 setigers (Blake and Ruff 2007).

Body: Unlike in other Opheliids, the body of *Ophelia assimilis* is not clearly regionated, although anterior ten setigers are abranchiate (Fauchald 1977; Blake and Ruff 2007).

Anterior: Anterior region inflated slightly. Ventral depression present, but not a true groove (Fig. 2). Prostomium pointed and triangular (Fig. 1).

Trunk: A mid-ventral groove is present from setiger eight to posterior (*Ophelia*, Fauchald 1977) (Fig. 2).

Posterior: Last three setigers with paired prominent dorsolateral ridges (Hartman 1969) (Fig. 3). Pygidium consists of a pair of large ventral lobes and about 11 smaller subglobular lobes in two crescents above the anal pore (Hartman 1969) (Fig. 3).

Parapodia: Low folds, biramous. Parapodia on first setiger are small and inconspicuous while the remaining setigers are larger. Interramal pores present. Middle parapodia ventrolateral and with crenulated branchiae (Fig. 4).

Setae (chaetae): All capillary and simple (Opheliidae, Fauchald 1977). Notosetae longer than neurosetae (Hartman 1969) (Fig. 4).

Eyes/Eyespots: None.

Anterior Appendages: None.

Branchiae: No branchiae on first 10 setigers or four posterior-most setigers (postbranchiate) between which there are 19 branchiate setigers (Fig. 1). The branchiae often disintegrate in preservation.

Burrow/Tube: *Ophelia assimilis* is an active burrower and does not inhabit a permanent burrow.

Pharynx: Bears an eversible and sack-like proboscis (not shown) which is unarmed and probably used for digging (Dales 1967).

Genitalia:

Nephridia: Six pairs of nephridiopores present on setigers 11–16 (branchial segments 2–7) (not shown).

Possible Misidentifications

Among the Opheliidae, there are at least six genera in our area, all of which are sand or mud dwellers with limited segmentation, simple prostomia, biramous parapodia and capillary setae.

Travisia spp. are cigar-shaped, without a ventral groove, but with branchiae and their posterior parapodia have large lobes.

Polyophthalmus spp. have a ventral groove along the whole body length, no branchiae but lateral eyes. They have a short anal tube with small anal cirri (Fauchald 1977).

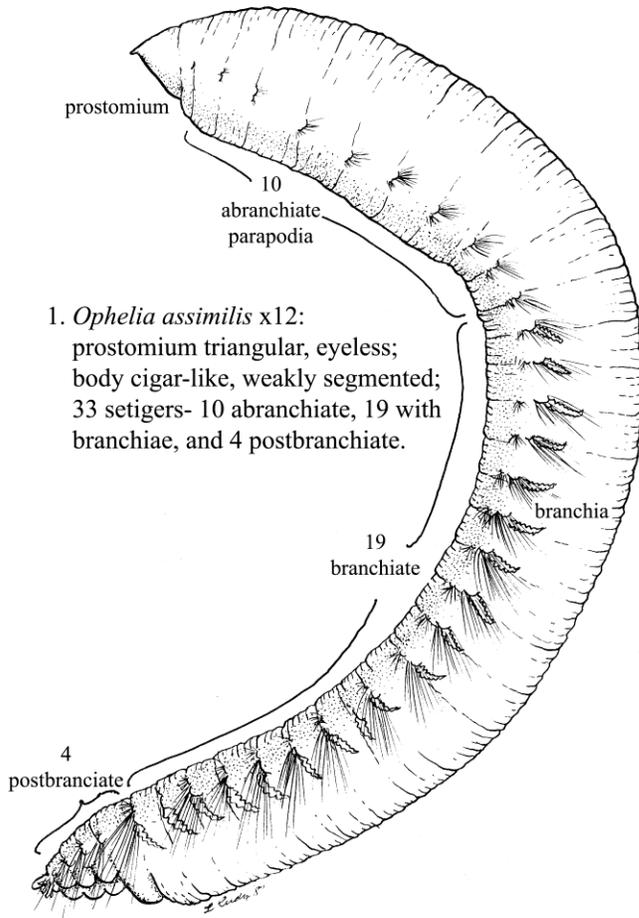
Ophelia spp. have a fusiform body morphology, inflated anterior and posterior ventral groove. They generally have branchiae on setigers 8–10.

Armandia spp. have a ventral groove along the whole body length, cirriform branchiae, lateral eyes and a long slender anal tube with paired long and internally attached ventral cirri and shorter dorsal cirri. *Armandia brevis* is the only local species in the genus *Armandia*.

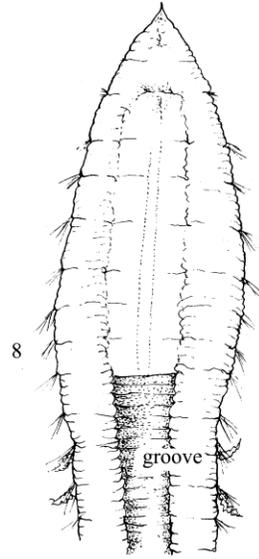
Thoracophelia (= *Euzonus*) spp. live on clean sandy beaches and have three distinct body regions, an inflated anterior set off from the thoracic region with a marked constriction and a narrow posterior with branchiae and a ventral groove.

Ophelina (= *Ammotrypane*) spp. are recognizable by a ventral groove along the

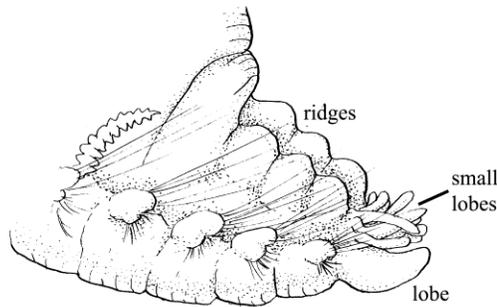
Ophelia assimilis



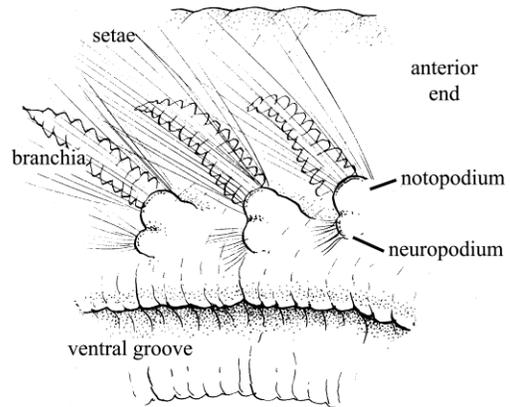
1. *Ophelia assimilis* x12:
prostomium triangular, eyeless;
body cigar-like, weakly segmented;
33 setigers- 10 abranchiate, 19 with
branchiae, and 4 postbranchiate.



2. Deep groove (anterior,
ventral view) x12: from setiger 8.



3. Pygidium (lateral view) x30:
3 dorsolateral ridges; a pair of
ventral lobes; smaller lobes above.



4. Some medial parapodia x30:
biramous parapodia, long notosetae;
crenulated branchiae.

whole body length (Fauchald 1977), cirriform branchiae only on posterior setigers, no lateral eyes and a long narrow anal tube with two internally attached ventral cirri (ibid). Two species occur in our area: *O. assimilis* and *O. pulchella* (Blake and Ruff 2007). *Ophelia pulchella* has 38 setigers, is 19–23 mm long. This species can be recognized from *O. assimilis*; it has nine abbranchiate anterior setigers, rather than 10 (Hartman 1969). It has a long conical prostomium and long flowing tufts of setae.

Ecological Information

Range: Type locality is Pacific Grove, California. Known range includes Oregon to California.

Local Distribution: Coos Bay, near bay mouth and Netarts Bay (Stout 1976).

Habitat: Clean sandy beaches. In Coos Bay, on spit near bay mouth in nearly marine conditions. Often found where current is strong (Wilson 1948).

Salinity: Found in full strength seawater (salinity 30).

Temperature:

Tidal Level: Intertidal, occurring at mid tide level where it is uncovered several hours each tide (England, Wilson 1948).

Associates: The razor clam, *Siliqua patula*, and olive snails (Olivellidae).

Abundance: Not common, but can be abundant locally and may have a narrowly dense distribution as in other local Opheliidae species.

Life-History Information

Reproduction: Eggs and sperm spawned into water. In similar species *O. bicornis* ripe eggs are dark green/brown.

Larva: Little is known about the larvae of *O. assimilis*. The larvae of *O. bicornis*, however, are trochophores with wide prototrohc and fairly short pelagic duration; metamorphosis occurs by day 19 as larvae attach to substrate by four anal papillae and parapodial lobes (Wilson 1948).

Juvenile:

Longevity:

Growth Rate:

Food:

Predators:

Behavior:

Bibliography

1. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In*: Light and Smith manual: intertidal invertebrates from central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.
2. DALES, R. P. 1967. Annelids. Hutchinson & Co., Ltd., London.
3. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. Natural History Museum of Los Angeles County Science Series. 28:1-190.
4. HARTMAN, O. 1969. Atlas of the Sedentariate Polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
5. STOUT, H., and S. V. SHABICA. 1976. The natural resources and human utilization of Netarts Bay, Oregon. Oregon State Universtiy, Corvallis, Oregon.
6. WILSON, D. P. 1948. The larval development of *Ophelia bicornis* Savigny. Journal of the Marine Biological Association. 27:540-553.

Updated 2014

Thoracophelia mucronata

A bloodworm

Phylum: Annelida
Class: Polychaeta
Order: Opheliida
Family: Opheliidae

Taxonomy: The genus *Thoracophelia* was revalidated in 2011 (Blake) and replaced the polychaete genus *Euzonus*, a junior homonym of the arthropod genus *Euzonus* (Brewer et al. 2011). For a brief period in 1956, *Thoracophelia* was a subgenus of *Euzonus* based on the presence or absence of pinnules on respiratory branchiae. Subgenera were deemed not necessary when research showed that pinnule development is an adaptation to habitat (Parke 1973; Blake 2011). *Thoracophelia mucronata* was described as *Ophelina mucronata*, but is more commonly seen under the name *Euzonus mucronata* or *Euzonus (Thoracophelia) mucronata*.

Description

Size: Typically 25–35 mm in length (maximum length around 50 mm) and 1–2 mm in width (Ricketts 1952).

Color: Iridescent and shimmering dark blue to dark red to purple. Some specimens have a pebbly surface. Males are more pinkish-red than the purple-red color found in reproductive females. This is likely due to the lower hemoglobin concentrations in male individuals (Law et al. 2013).

General Morphology: Small opheliid worms with red color and slender body that tapers to a point anteriorly and posteriorly (Fig. 1).

Body: The body of *Thoracophelia* species consists of 38 segments (Dales 1952) and can be divided into three body regions (Blake 2011; Law et al. 2013).

Anterior: Triangular head (Ricketts 1952) (Fig. 4). The cephalic region includes the prostomium and setigers one and two and is set off from the rest of the body by a constriction (head, Fig. 1). The mouth is a small slit that is found ventral of the first setiger (McConnaughey and Fox 1949).

Trunk: A mantle covers the first eight segments and the thoracic region (setigers 2–10) is rather swollen (Blake 2011). The setigers are distinctly marked with several muscle bands between them.

Posterior: The posterior body region is long and narrow and exhibits a well-defined ventral groove is limited to the posterior area (Fig. 1) (Blake 2011; Law et al. 2013). Pygidium pointed with a large ventral cirrus (McConnaughey and Fox 1949) and 6–7 lateral cirri that surround the anus (McConnaughey and Fox 1949).

Parapodia: Small, simple, biramous (family Opheliidae, Blake and Ruff 2007).

Setae (chaetae): Simple, and hair-like. Second somite chaetae and those in posterior telescoping segments are longer than the other body regions (McConnaughey and Fox 1949).

Eyes/Eyespots: Three asymmetrical eyes are present in the brain area (McConnaughey and Fox 1949).

Anterior Appendages: None.

Branchiae: Parapodial branchiae are branched and biramous and simple (without pinnules or not feather-like) (Fig. 2). Branchiae are found on the posterior middle two-thirds of the body (Ricketts 1952) but not the posterior most segments (Blake 2011).

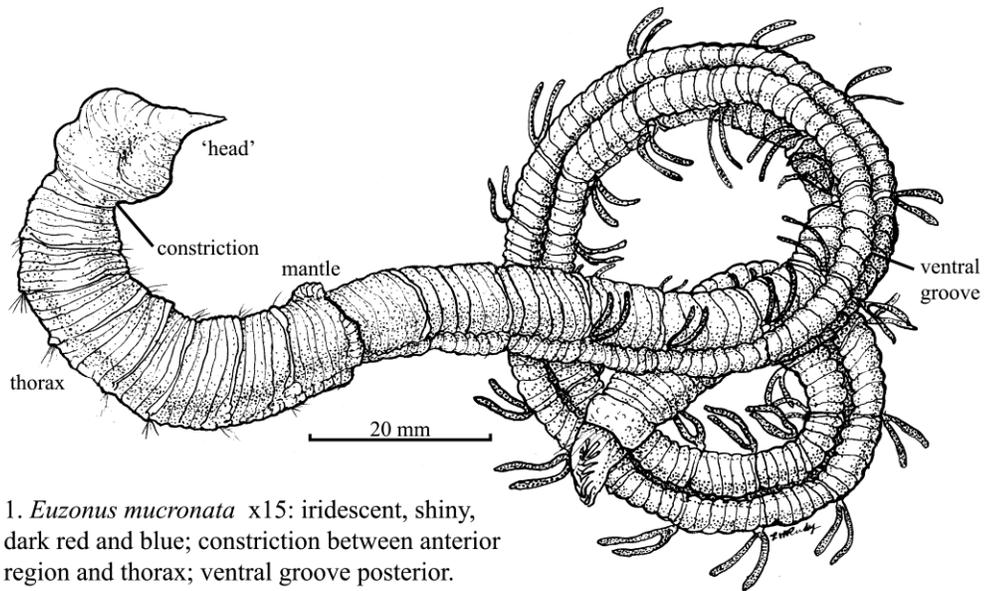
Burrow/Tube: *Thoracophelia mucronata* is an active burrower and does not inhabit a permanent burrow.

Pharynx: Consists of three soft, ciliated lobes and bears eversible proboscis (McConnaughey and Fox 1949; Dales 1952) (Fig. 3).

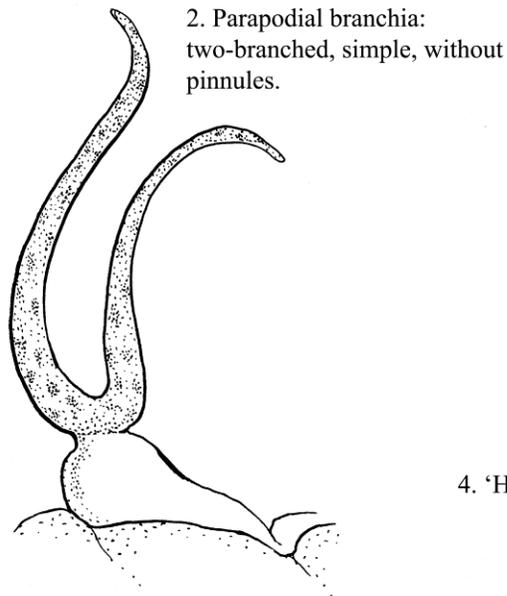
Genitalia:

Nephridia: Protonephridial and found from the fifth branchial segment to the 1st post-branchial segment (McConnaughey and Fox 1949).

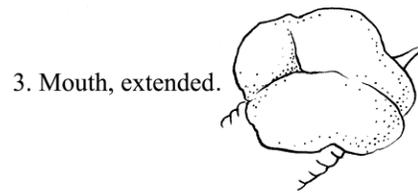
Thoracophelia mucronata



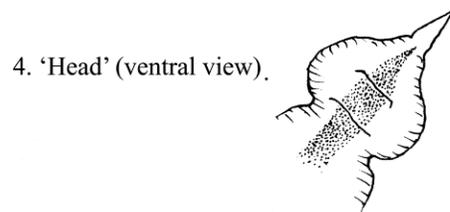
1. *Euzonus mucronata* x15: iridescent, shiny, dark red and blue; constriction between anterior region and thorax; ventral groove posterior.



2. Parapodial branchia: two-branched, simple, without pinnules.



3. Mouth, extended.



4. 'Head' (ventral view).

Possible Misidentifications

Among the Opheliidae, there are at least six genera in our area, all of which are sand or mud dwellers with limited segmentation, simple prostomia, biramous parapodia and capillary setae.

Ophelina (= *Ammotrypane*) spp. have a ventral groove along the whole body length (Fauchald 1977), cirriform branchiae only on posterior setigers, no lateral eyes and a long narrow anal tube with two internally attached ventral cirri (ibid).

Travisia spp. are cigar-shaped, without a ventral groove but with branchiae and their posterior parapodia have large lobes.

Polyopthalmus spp. have a ventral groove along the whole body length, no branchiae but lateral eyes. They have a short anal tube with small anal cirri (Fauchald 1977).

Ophelia spp. have a fusiform body morphology, inflated anterior and posterior ventral groove. They generally have branchiae on setigers 8–10.

Armandia spp. have a ventral groove along the whole body length, cirriform branchiae, lateral eyes and a long slender anal tube with paired long and internally attached ventral cirri and shorter dorsal cirri. *Armandia brevis* is the only local species in the genus *Armandia*.

Thoracophelia (= *Euzonus*) spp. live on clean sandy beaches and can be recognized by three distinct body regions, an inflated anterior set off from the thoracic region with a marked constriction and a narrow posterior with branchiae and a ventral groove. Other *Thoracophelia* species to be found on sandy beaches include *T. williamsi* and *T. dillonensis* and species can be differentiated by their branchial structure. There are 18 pairs of dorsal branchiae in *T. mucronata* which are bifurcating while in *T. williamsi* have 2–3 main branches (16–17 total branchial pairs, Law et al. 2013), one or more bearing side branches and lateral pinnules. *Thoracophelia dillonensis* has single, not double branchiae (15 pairs, Law et al. 2013), with 15–20 pectinate divisions on one side “resembling a comb” (Kozloff 1993). (see Fig. 1 Law et al. 2013).

Ecological Information

Range: Type locality is southern California (Blake 2011). Range includes British Columbia to northern Baja California.

Local Distribution: Clean sand of outer shore beaches and bays including in Coos Bay Crown Point, Fossil Point and North Bay. Also in Cape Arago beaches.

Habitat: Clean sand exposed to high wave action, where populations can shift after strong storm events (Dales 1952). The “inhabitant par excellence” of the protected beaches (Ricketts 1952).

Salinity:

Temperature:

Tidal Level: Mid to higher intertidal and may correspond to worm age (Dales 1952).

Associates:

Abundance: Often found in dense mats of many hundreds of thousands of worms.

Thoracophelia mucronata can be found in a narrow band (less than 1 m wide) at the mid tide line marked with tiny holes in the surface sand. Within this band, worms can be abundant and reach densities of 100 individuals 10/cm² (Kozloff 1993). Densities of over 40,000/m² have been reported in southern California (McConnaughey and Fox 1949).

Life-History Information

Reproduction: Dioecious and atokous.

Spawning takes place in summer months, April to September (southern California, Dales 1952), oocytes are 65 µm in diameter and disc-shaped. Development occurs quickly with embryos reaching 16-cell stage after just two hours (15–18° C, Dales 1952).

Larva: Young trochophore larvae are non-feeding and begin swimming at six hours post fertilization (Dales 1952). By five days the larvae are 100µm in length and possess an equatorial prototroch, a posterior telotroch and a pair of eyes. Settlement of two-setiger larvae begins after 10 days (McConnaughey and Fox 1949; Dales 1952; Fernald et al. 1987).

Juvenile: The larval apical tuft is lost after 10 days and the proboscis is fully formed and eversible when juveniles are 1.0 mm in length. The prostomium becomes pointed and marked from the thoracic region when they reach a length of 2.0 mm when ventral and posterior adhesive anal papillae are

present and the juvenile bears 25 chaetigerous segments. Between these four papillae the adult cirrus will grow from the pygidium (Dales 1952). The total number of adult segments has been reached (38) once juveniles are 5.0 mm in length.

Longevity:

Growth Rate: Little is known about the growth rate, but individuals continue to grow in length with age (Dales 1952).

Food: Deposit feeders. Micro-organisms filtered from and having been attached to fine sands in which they burrow much as to earthworms.

Predators: Shore birds (e.g. sandpipers, godwits and curlews) (McConnaughey and Fox 1949).

Behavior: As is true for other members of the Opheliidae, *T. mucronata* is an active and rapid burrower and, when the tide is out, occur buried as deep as 20 cm (Kozloff 1993).

Bibliography

1. BLAKE, J. A. 2011. Revalidation of the genus *Thoracophelia* Ehlers, 1897, replacing *Euzonus* Grube, 1866 (Polychaeta: Opheliidae), junior homonym of *Euzonus* Menge, 1854 (Arthropoda: Diplopoda), together with a literature summary and updated listing of *Thoracophelia* species. *Zootaxa*:65-68.
2. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In*: Light and Smith manual: intertidal invertebrates from central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.
3. BREWER, M. S., P. SIERWALD, and J. E. BOND. 2011. A generic homonym concerning chordeumatid millipedes (Arthropoda: Diplopoda) and ophellid worms (Annelida: Polychaeta). *Zootaxa*. 2744:65-68.
4. DALES, R. P. 1952. The larval development and ecology of *Thoracophelia mucronata* (Treadwell). *The Biological Bulletin*. 102:232-242.
5. FAUCHALD, K. 1977. The Polychaete worms: definitions and keys to the orders, families and genera. Natural History Museum of Los Angeles County, Los Angeles.
6. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
7. HARTMAN, O. 1969. Atlas of the sedentary polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
8. KOZLOFF, E. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
9. LAW, C. J., K. M. DORGAN, and G. W. ROUSE. 2013. Validation of three sympatric *Thoracophelia* species (Annelida: Opheliidae) from Dillon Beach, California using mitochondrial and nuclear DNA sequence data. *Zootaxa*. 3608:67-74.
10. MCCONNAUGHEY, B. H., and D. L. FOX. 1949. The anatomy and biology of the marine polychaete *Thoracophelia mucronata* (Treadwell) Opheliidae. *University of California Publications in Zoology*. 47:318-340.
11. PARKE, S. R. 1973. Biological aspects of speciation in three sympatric *Euzonus* species at Dillon Beach, California (Polychaeta: Opheliidae). M.S. University of the Pacific, Stockton.
12. RICKETTS, E. F. 1952. Between Pacific tides: an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific coast between Sitka, Alaska, and Northern Mexico. Stanford: Stanford University Press, Stanford.

Updated 2014

Leitoscoloplos pugettensis

A burrowing polychaete worm

Phylum: Annelida
Class: Polychaeta
Order: Orbiniida
Family: Orbiniidae

Taxonomy

In 1957 Pettibone determined that *H. elongatus* was a homonym a different species named *H. elongatus* and was therefore renamed *H. pugettensis* (Blake 1980). *Haploscoloplos* became a junior synonym of *Scoloplos* (for nomenclature see Blake 1980) in 1977 and the genus *Leitoscoloplos* was erected which now includes all former *Haploscoloplos* species with pointed thoracic setae and without parapodial hooks, including *L. pugettensis*.

Description

Size: Individuals range in size from 100–200 mm in length and 3 mm in width (Hartman 1969) with up to 300 setigers (Blake 1996). The specimen examined from Coos Bay was 75 mm long with 136 segments.

Color: When sexually mature, males are pink and females grey (Blake 1980).

General Morphology: Orbiniids can be recognized by their body morphology: anterior region is firm while the abdominal region is fragile, ragged and easily lost and by the presence of camerated and crenulated setae (Blake and Ruff 2007).

Body: Long, slender with 200–300 short segments (Johnson 1901). Body most broad at segments 9–17, narrowing gradually after segment 200.

Anterior: Prostomium small, acutely pointed and conical (genus *Leitoscoloplos*, Day 1977) and with small palpode at apex (Fig. 2a). Peristomium bears one ring and width increases rapidly toward the second segment (Fig. 2a). First segment achaetous (Figs. 1, 2).

Trunk: Thorax composed of 14–21 setigers with transition from thoracic to abdominal region between setigers 15–21 (Hartman 1969). Thoracic dorsum flat and ventrum convex. No ventral papillae in posterior thorax

(genus *Leitoscoloplos*, Day 1977) (Fig. 1).

Posterior: Pygidium slightly expanded, hemispherical). Anus dorsal. Long, slender anal cirri (*Scoloplos acmeceps*, Fig. 1, Johnson 1901).

Parapodia: Biramous and lateral anteriorly (family Ordiniidae, Fauchald 1977), dorsal posteriorly (Hartman 1969) (Fig. 1). Anterior-most podia short. Thorax with small papillar postsetal lobes (Hartman 1969) (Fig. 3). Abdominal parapodia supported by acicula (Fig. 5) and lobes become long and leaf-like posteriorly (Johnson 1901) (Fig. 5).

Abdominal notopodia with subtriangular postsetal lobes (Blake 1996). Abdominal neuropodia with bifid lobes. Inflated neuropodial flange present (Blake 1996).

Setae (chaetae): Simple (not jointed) (family Orbiniidae Fauchald 1977). All slender and pointed: *leitos* = simple, *scoloplos* = thorn (Day 1977). Notosetae and neurosetae finely crenulate (Blake 1996) in thorax (Fig. 4a). Abdominal capillary noto- and neurosetae, as in thorax, have few furcate spines (Hartman 1969) (Fig. 4c).

Eyes/Eyespots: None.

Anterior Appendages: None (family Orbiniidae, Fauchald 1977).

Branchiae: Begin on setigers 13–18 (Hartman 1969). Setiger 18 in present specimens (from Coos Bay). Branchiae small (i.e. short and narrow) anteriorly, becoming flat and subdistally inflated, laterally fringed (“fimbriated”) and larger posteriorly (Fig. 5) (Hartman 1969). Abdominal branchiae are twice as long as notopodial lobes (Blake 1996).

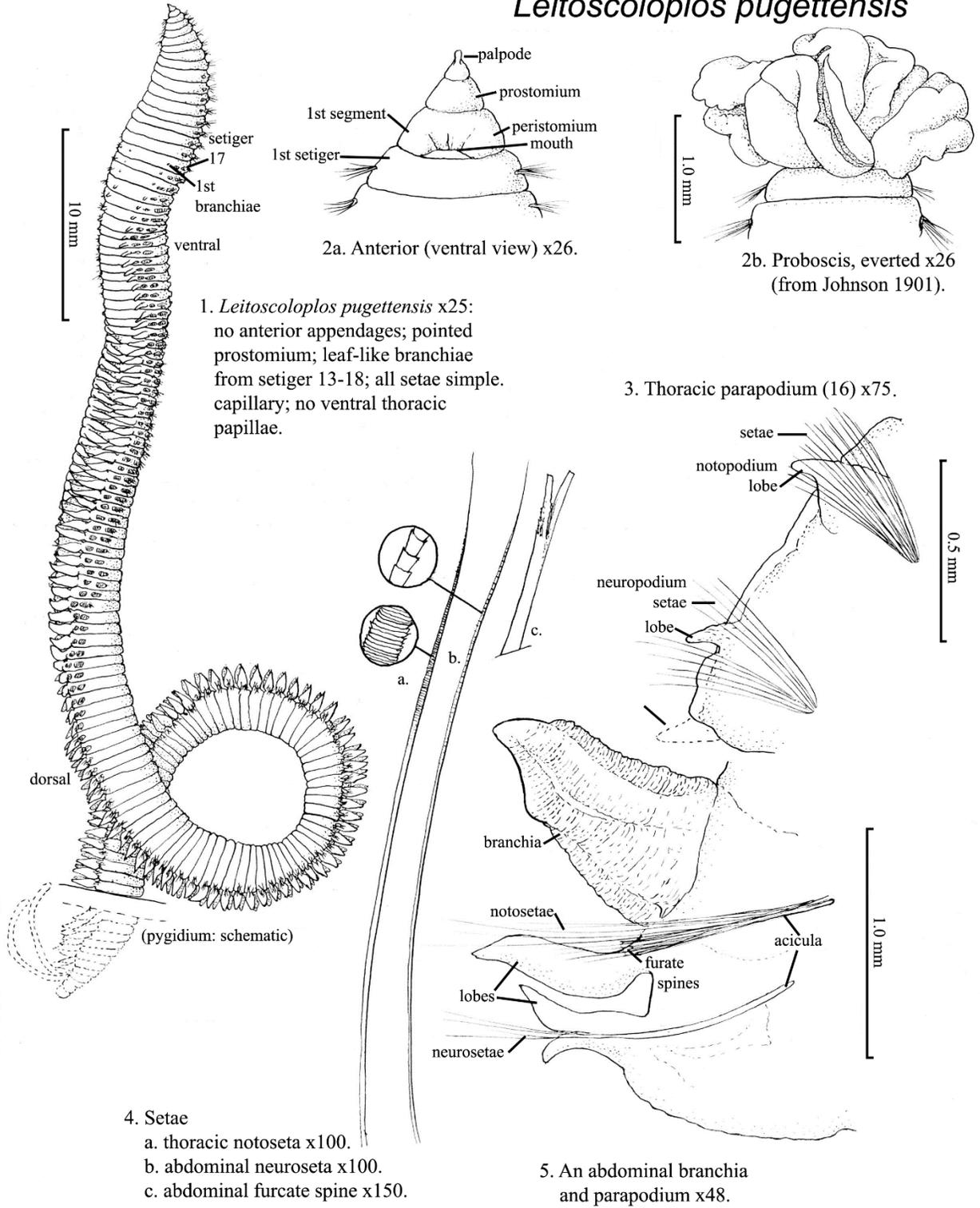
Burrow/Tube: These burrowing polychaetes do not inhabit permanent burrows or tubes (Blake and Ruff 2007).

Pharynx: Bears eversible proboscis with leaf-shaped lobes (Fig. 2b).

Genitalia:

Nephridia:

Leitoscoloplos pugettensis



1. *Leitoscoloplos pugettensis* x25:
no anterior appendages; pointed
prostomium; leaf-like branchiae
from setiger 13-18; all setae simple.
capillary; no ventral thoracic
papillae.

2a. Anterior (ventral view) x26.

2b. Proboscis, everted x26
(from Johnson 1901).

3. Thoracic parapodium (16) x75.

4. Setae
a. thoracic notoseta x100.
b. abdominal neuroseta x100.
c. abdominal furcate spine x150.

5. An abdominal branchia
and parapodium x48.

Possible Misidentifications

The order Orbiniida (Fauchald 1977) includes the families Orbiniidae and Paraonidae, the latter comprising smaller species (less than 20 mm in length) (Blake and Ruff 2007). The order is characterized by a lack of prostomial appendages, maximum of two asetigerous anterior segments, a lack of additional cephalized segments or palps, simple setae and an eversible pharynx that is either an axial sac or biramous (Fauchald 1977). Members of the family Orbiniidae have a prostomium and peristomium without appendages, one to two asetigerous anterior segments and lateral thoracic parapodia, becoming dorsal abdominally. Setae can be capillary or simple hooks and some species have brush-topped bifid or furcate setae. Orbiniidae and Paraonidae can be distinguished by peristomial rings, where orbiniids have one and paraonids have two (Blake 2000).

There are several similar families (not in the order Orbiniida): Ophelidae are short and stout and have a strong ventral groove. Goniadidae and Glyceridae have palps or some kind of buccal appendage.

Ampharetidae have retractible tentacles and *Lumbrineridae* have hard jaw pieces and hooded hooks among the setae (uncini).

Among those families which are orbiniids, the Paraonidae are small and often overlooked, they have branchiae occurring only on maximum of 15–20 segments, beginning on setigers 4–10 (not on all posterior segments). The body in Paraonidae is not divided into distinct regions by setae and parapodial shapes, but changes gradually along the body (not distinctly as in Orbiniidae, Fauchald 1977). A Paraonidae prostomium can have a medial antenna, which are lacking in Orbiniidae. They have branchiae on some median setigers in most species. The parapodia are lateral. Local paraonid genera include: *Aricidea*, *Cirrophorus*, *Paraonella* and *Levinsenia* (= *Tauberia*) (Hobson and Banse 1981; Blake and Ruff 2007).

Orbiniidae genera in the subfamily Protoarciinae are small (less than 20 mm), have rounded prostomium, 1–2 asetigerous anterior segments, two peristomial rings and can lack branchiae. Recent research suggests that many Protoarciinae species are

simply juvenile orbiniids (Blake 1996; 2000b). Genera include:

Orbiniella, with two asetigerous anterior segments and no branchiae. Neuropodia have both hooks and capillary setae (Hobson and Banse 1981). *Orbiniella nuda* is found intertidally in Washington and British Columbia, amongst gravel and rock.

Paraorbiniella, a monotypic northeastern Pacific genus (Hobson and Banse 1981).

Protoarcia spp. have two asetigerous segments, are less than 6 mm in length and have been found in northern California (Blake 1975).

Protoarciella differs from *Protoarcia* by the presence of neuropodial hooks in the abdominal region (Hobson and Banse 1981). Most notosetae are forked. Its branchiae begin at setigers 4–5 and continue to setigers 28–47. *Protoarciella oligoranchia* is found in British Columbia (Hobson 1976).

Polychaetes in the subfamily Orbiniinae (including *L. pugettensis*) have only 1 asetigerous anterior segment and its members are usually over 20 mm in length. Local genera in the Orbiniinae include:

Naineris, which has a broadly rounded prostomium (unlike that of *Leitoscoloplos*). *Naineris dendritica*, often found in algae or in the marine grass (*Phyllospadix*), occurs inside Coos Bay (Hartman and Reish 1950) and offshore. *Naineris quadricuspida* and *N. uncinata* are found farther north (Hobson and Banse 1981).

Orbinia have pointed prostomium and one asetigerous anterior segment (as in *L. pugettensis*), but they also have very conspicuous ventral papillae on the posterior thoracic segments, which are lacking in *L. pugettensis*. *Orbinia johnsoni* is a rocky intertidal species.

Scoloplos is the genus most likely to be confused with *Leitoscoloplos*. *Scoloplos* spp. have a pointed prostomium, one asetigerous anterior segment and no ventral thoracic papillae. These two genera must be separated by their setae: *Scoloplos* have blunt spines as well as slender pointed setae in the thoracic neuropodia. *Scoloplos acmeceps* has a few incomplete rows of curved and ridged uncini in its thoracic neuropodia. Some of these neuropodia also have a single post-setal lobe. This species is

found in the Coos Bay and Umpqua estuaries, usually subtidally. In California, it is also intertidal, in mud and algae holdfasts and in *Zostera* roots (Blake 1975). *Scoloplos armiger*, found in southern California, is distinguished from the former species by the presence of two post-setal thoracic neuropodial lobes (not one).

In *Leitoscoloplos* the thorax is rounded and lacks parapodial hooks and ventral papillae. There is only one other known Pacific northeast species, *L. panamensis* which occurs from British Columbia to Panama. This species can have one or two subpodial lobes on its posterior thoracic parapodia (Fig. 3, dotted lines, arrow), which are lacking in *L. pugettensis*. Branchiae begin on setigers 11–13 in *L. panamensis* and on setigers 13–18 in *L. pugettensis*.

Ecological Information

Range: Alaska to southern California (Hartman 1969).

Local Distribution: In Coos Bay including South Slough, Shore Acres and offshore. Also Columbia River mouth and Yaquina Bay.

Habitat: Burrows in sandy shores (Johnson 1901) in gravelly, silty, fine sands (Parkinson 1978) or fine mud (Barnard and Reish 1959). Individuals found in most substrates except for black sulfide mud. Found occasionally with eelgrass or algae, but not as closely associated with plant growth as in Naineris (Blake 1975). In Bodega Bay, California, most common in sandy mud with a large grain size and with little algal (*Ulva*) cover (Parkinson 1978).

Salinity: Found in salinities of 30 in Coos Bay.

Temperature: Larvae successfully cultured at 14–15°C (Blake 1980).

Tidal Level: Near low-water mark (Johnson 1901). Also subtidal, but not as often as *Scoloplos* in Coos Bay, down to 380 m (Parkinson 1978).

Associates:

Quantitative Information

Abundance: One of the most common intertidal and subtidal benthic polychaetes of the Pacific Coast of North America (Blake 1980). A stable population (12 months, Tomales Bay, California) is most dense October through December and March

through April. Size distribution also stable (Blake 1980). Most frequently found Orbinii in Newport Bay, California (Barnard and Reish 1959) and in northern California (Day 1977).

Life History Information

Reproduction: Dioecious. Individuals may pair up during spawning where males and females release gametes with fertilize externally (Blake 1980). Ripe females are found June through December (Tomales Bay, California), with largest number found in July. Females form a 2 cm pear-shaped cocoon at sediment surface and secrete a jelly-like substance from ventrum. Eggs are extruded from medial segments through nephridial pores at notopodial bases where deposition takes 1–2 hrs. After spawning, the female stretches a portion of the jelly mass and anchors it to the sediment. Through this thin, hollow extension the larvae will eventually escape from the cocoon. Eggs are large and yolky with average egg diameter is 210 µm.

Larva: Development is described in Blake (1980) at 15° C where trochophore larvae develop at two days post fertilization. Larvae are barrel-shaped and have two red eyes. At four days, trochophore larvae are 290 µm in length. Larvae are metatrochophores between five and eight days. At 11 days they are three setiger nectochaetes and hatch from 3–12 setiger stage between 11 and 20 days. A few larvae escape at a seven segment state and swim, but most crawl, lacking swimming cilia at 12 segments (Blake 1980). A single achaetous peristomial ring (which defines members of the Orbininae) develops early (Blake 2000b).

Juvenile: Juveniles can be maintained to sexual maturity on a diet of homogenized *Enteromorpha*. Juvenile *L. pugettensis* have 10 setigers at 17 days (880 µm long) and 13 setigers at 22 days (1010 µm long) at which point they have a fully functional proboscis. The anterior epidermis is yellowish, has two red eyes and one achaetous segment (the first segment). The body is granular in texture and branchiae begin on setigers 8–10. Notosetae are longer than neurosetae and there are two short anal cirri that elongate at 22 days (Blake 1980).

Longevity:

Growth Rate: At six days a three segment larva is approximately 5 mm, at 14 days a 10 segment larva is 9 mm, at 21 days a 14 segment larva is 12 mm (15° C and 33, Blake 1980).

Food: All Orbiniids are considered to be non-selective deposit feeders because they have a sac-like pharynx, but no work has been done to test for selectivity (Fauchald and Jumars 1979). Gut contents include diatoms, foraminifera and sand (Parkinson 1978).

Predators:

Behavior: A free burrower with pointed prostomium used as anchor to penetrate substrate and to enlarge burrow (Parkinson 1978). The muscular thorax is used for digging and the soft proboscis is not. Movement is by retrograde waves, back or forward much like in *Arenicola marina* (Parkinson 1978). Larva burrows with pharynx (Fauchald and Jumars 1979).

Bibliography

1. BARNARD, J. L., and D. J. REISH. 1959. Ecology of amphipoda and polychaeta of Newport Bay, California. University of Southern California Press, Los Angeles, Calif.
2. BLAKE, J. A. 1975. Phylum Annelida: Class Polychaeta, p. 151-243. *In:* Lights manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
3. —. 1980. The larval development of polychaeta from the northern California coast. IV. *Leitoscoloplos pugettensis* and *Scoloplos acmeceps* (Family Orbiniidae). *Ophelia*. 19:1-18.
4. —. 1996. Family Orbiniidae, p. 1-26. *In:* Taxonomic atlas of the benthic fauna of Santa Maria Basin and Western Santa Barbara Channel. Vol. 6. J. Blake, B. Hilbig, and P. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
5. —. 2000. A new genus and species of polychaete worm (Family Orbiniidae) from methane seeps in the Gulf of Mexico, with a review of the systematics and phylogenetic interrelationships of the genera of Orbiniidae. *Cahiers de Biologie Marine*. 41:435-449.
6. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In:* Light and Smith manual: intertidal invertebrates from central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.
7. FAUCHALD, K. 1977. The Polychaete worms: definitions and keys to the orders, families and genera. Natural History Museum of Los Angeles County, Los Angeles.
8. FAUCHALD, K., and P. A. JUMARS. 1979. Diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology*. 17:193-284.
9. HARTMAN, O. 1969. Atlas of the sedentariate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
10. HARTMAN, O., and D. J. REISH. 1950. The Marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
11. HOBSON, K. D. 1976. *Protoariciella oligobranchia* new species (Orbiniidae) and six new records of Orbiniidae, Questidae, and Paraonidae (Annelida, Polychaeta) from British Columbia. *Canadian Journal of Zoology*. 54:591-596.
12. HOBSON, K. D., and K. BANSE. 1981. Sedentariate and archiannelid polychaetes of British Columbia and Washington. *Canadian Bulletin of Fisheries and Aquatic Sciences*. 209:1-144.
13. JOHNSON, H. P. 1901. The Polychaeta of the Puget Sound region. *Proceedings of the Boston Society of Natural History*. 29:381-437.
14. PARKINSON, G. T. 1978. Aspects of feeding, burrowing, and distribution of *Haploscoloplos elongatus* (Polychaeta: Orbiniidae) at Bodega Harbor, California. *Pacific Science*. 32:149-155.

Updated 2014

Paraonella platybranchia

Phylum: Annelida
Class: Polychaeta
Order: Orbiniida
Family: Paraonidae

Description

Size: Individuals approximately 15 mm in length (Hartman 1969) to 0.45 mm in width (Hobson 1976) with 65–120 segments. The specimen (from Coos Bay) dissected for this description 8 mm long and 0.3 mm wide.

Color: Pale translucent with green tinge post-branchially (Hartman 1961).

General Morphology: Long, slender and threadlike (Hartman 1961).

Body: Segments wider than long and body regions not distinctly divided (Paraonidae).

Anterior: Prostomium long (sp. *platybranchia*, Hartman 1961), triangular and acute with anterior half set off by marked constriction (Fig. 2). A pair of nuchal elevations is present on sides of peristomium near mouth (genus *Paraonella*, Fauchald 1977). Mouth is a triangular slit between prostomium and first segment (Fig. 2) with posterior long notch that forms lower lip (Hartman 1961).

Trunk:

Posterior: Pygidium is a flat, auricular ventral lobe about twice as wide as the last posterior segment (Fig. 1). Three cirriform processes (two lateral and one shorter, midventral) attached dorsally to lobe (Hobson 1976) are easily lost. Anal pore dorsal.

Parapodia: Present on all segments, bearing short setigerous papillae. Notopodia short to long notosetal lobes, which are longest in branchial segments (Hartman 1969) and begin on setiger four (Fig. 3).

Setae (chaetae): All segments are setigerous (Fig. 1). Setae are all long, capillary and hair-like (*Paraonella*, Hobson and Banse 1981). No acicular spines (as in *Nereis vexillosa*). Limbate notosetae (2–4) on first 3–5 notopodia and first 13–14 neuropodia (Hobson 1976). In branchial segments, notosetae exist in less dense fascicles than neurosetae.

Eyes/Eyespots: One small pair at base of posterior half of prostomium (sp. *platybranchia*, Hartman 1961). Some specimens (including the individual used for this description) with accessory eyespots (Posey 1985) (Fig. 2).

Anterior Appendages: None.

Branchiae: Branchiae broad, flat, distally pointed, lying flat across dorsum, just meeting (Fig. 2) consisting of 16–29 branchial pairs (18 in the present specimen) beginning on setiger four. *Platybranchia* = plate-like branchiae.

Burrow/Tube:

Pharynx: Bears short, eversible and sac-like proboscis (Fauchald and Jumars 1979).

Genitalia:

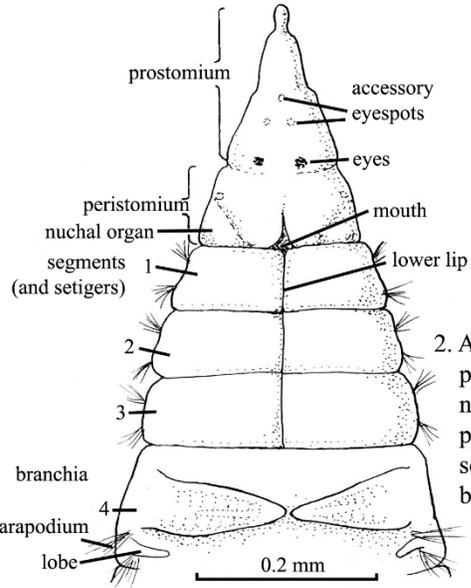
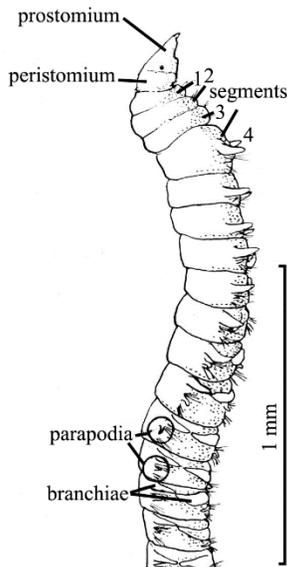
Nephridia:

Possible Misidentifications

The order Orbiniida (Fauchald 1977) includes the families Orbiniidae and Paraonidae (and the “enigmatic” Questidae (Bleidorn 2005)), the latter comprising smaller species (less than 20 mm in length) (Blake and Ruff 2007). The order is characterized by a lack of prostomial appendages, maximum of two asetigerous anterior segments, a lack of additional cephalized segments or palps, simple setae and an eversible pharynx that is either an axial sac or biramous (Fauchald 1977). Members of the family Orbiniidae have a prostomium and peristomium without appendages, 1–2 asetigerous anterior segments and lateral thoracic parapodia, becoming dorsal abdominally. Setae can be capillary or simple hooks and some species have brush-topped bifid or furcate setae. Orbiniidae and Paraonidae can be distinguished by peristomial rings: orbiniids have one and paraonids have two (Blake 2000a, b).

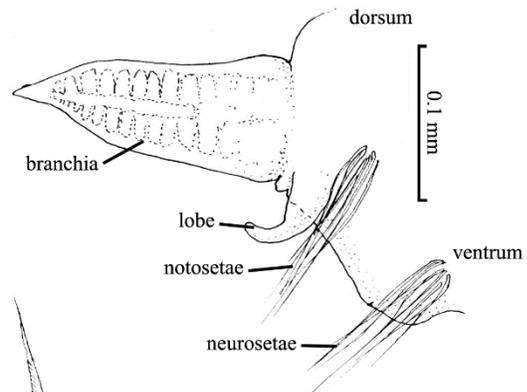
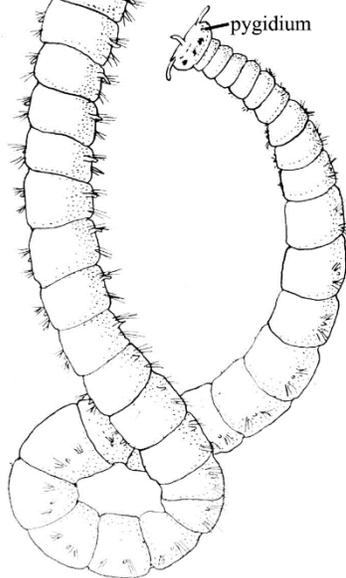
There are several similar families (not in the order Orbiniida): Ophelidae are short and stout and have a strong ventral groove. Goniadidae and Glyceridae have palps or some kind of buccal appendage. Ampharetidae have retractible tentacles and

Paraonella platybranchia

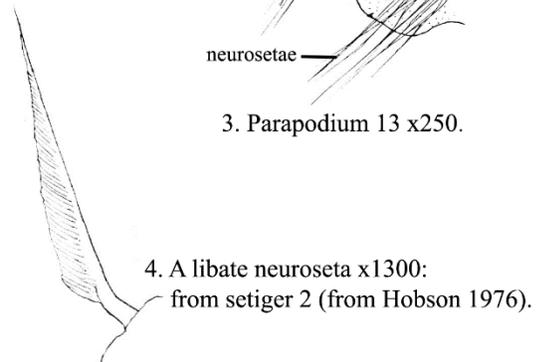


2. Anterior (dorsal view) x150: prostomium long, narrow, 2 eyes; nuchal organs, mouth on peristomium long lower lip; all segments setigerous; branchiae begin on setiger.

1. *Paraonella platybranchia* (L:15mm) x50: slender, threadlike; 65-75 segments; 16-29 pairs flat, pointed branchiae; acute prostomium without appendages; pygidium a flange with three cirriform processes.



3. Parapodium 13 x250.



4. A libate neuroseta x1300: from setiger 2 (from Hobson 1976).

Lumbrineridae have hard jaw pieces and hooded hooks among the setae (uncini).

The Paraonidae are small and often overlooked, they have branchiae occurring only on maximum of 15–20 segments, beginning on setigers 4–10 (not on all posterior segments). The body in Paraonidae is not divided into distinct regions by setae and parapodial shapes, but changes gradually along the body (not distinctly as in Orbiniidae, Fauchald 1977). A Paraonidae prostomium can have a medial antenna, which are lacking in Orbiniidae. They have branchiae on some median setigers in most species. The parapodia are lateral.

Paraonella platybranchia is the only local species in the genus *Paraonella*, other local paraonid genera include (Hobson and Banse 1981; Blake and Ruff 2007):

Aricidea spp, have a medial prostomial antenna, but they have modified setae in all species in the postbranchial neuropoda. Gills begin on setiger four in this genus (Hobson and Banse 1981). At least seven species occur in the northeast Pacific.

Cirrophorus spp. have medial and posterior notopodia which are forked or acicular, unlike other genera of this family. They can have a short medial antenna. *C. branchiata* (= *Aricidea* Berkely and Berkeley) and *C. lyra* (Southern) (= *Paraonis* Banse and Hobson 1968) are both found in the northeastern Pacific (Hobson and Banse 1981).

The cosmopolitan *Levinsenia* (= *Tauberia*), like *Paraonella*, has no medial prostomial antenna. It does have hooded hooks in its postbranchial neuropodia, which *Paraonella* lacks.

Ecological Information

Range: Type locality is San Diego. Pacific coast from British Columbia and Washington (Hobson and Banse 1981), Oregon, California (Hartman 1961; Blake and Ruff 2007) to Panama (Hobson 1976). Also in Columbia River mouth (Blake and Ruff 2007).

Local Distribution: In Coos Bay, South Slough and subtidally offshore and in Coos Bay channel.

Habitat: This species prefers clean, fine sand (intertidally in Coos Bay and offshore).

Also in muddy, coarse sand (San Diego, Hartman 1969).

Salinity: Found in salinities of 30 in Coos Bay.

Temperature:

Tidal Level: Intertidal (in South Slough) to subtidal.

Associates: In San Diego associates include other polychaetes: *Prionospio malmgreni*, *Dispio uncinata*, *Nephtys caecoides*, *Eteone* sp.

Abundance:

Life-History Information

Reproduction: Two oval or round eggs/segment post-branchially (Hobson 1976) where each egg is 190–230 µm in diameter.

Larva: The development and larva are unknown for local paraonids (Crumrine 2001).

Juvenile:

Longevity:

Growth Rate:

Food: Probably a non-selective, burrowing deposit-feeder or surface feeder (Fauchald and Jumars 1979). Searches ripple troughs or sand for plant debris and dead animals including: pennate diatoms, foraminifera, small crustaceans.

Predators:

Behavior: Posterior end burrows corkscrew fashion into sediment making characteristic spiral patterns (also seen in fossil record) (Fauchald and Jumars 1979). Worm often curled when found (Posey 1985).

Bibliography

1. BANSE, K., and K. D. HOBSON. 1968. Benthic polychaetes from Puget Sound, Washington, with remarks on four other species. Proceedings of the United State National Museum. 125:1-53.
2. BLAKE, J. A. 2000a. A new genus and species of polychaete worm (Family Orbiniidae) from methane seeps in the Gulf of Mexico, with a review of the systematics and phylogenetic interrelationships of the genera of Orbiniidae. Cahiers de Biologie Marine. 41:435-449.

3. —. 2000b. Family Orbiniidae, p. 1-22. *In*: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
4. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
5. BLEIDORN, C. 2005. Phylogenetic relationships and evolution of Orbiniidae (Annelida, Polychaeta) based on molecular data. *Zoological Journal of the Linnean Society*. 144:59-73.
6. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
7. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County Science Series*. 28:1-190.
8. FAUCHALD, K., and P. A. JUMARS. 1979. Diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology*. 17:193-284.
9. HARTMAN, O. 1961. Polychaetous annelids from California, p. 226 p., [1] leaf of plates. *In*: Allan Hancock Pacific expeditions, v. 25. University of Southern California Press, Los Angeles, Calif.
10. —. 1969. Atlas of the sedentariate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California Los Angeles.
11. HOBSON, K. D. 1976. *Protoariciella oligobranchia* new species (Orbiniidae) and six new records of Orbiniidae, Questidae, and Paraonidae (Annelida, Polychaeta) from British Columbia. *Canadian Journal of Zoology*. 54:591-596.
12. HOBSON, K. D., and K. BANSE. 1981. Sedentariate and archiannelid polychaetes of British Columbia and Washington. *Canadian Bulletin of Fisheries and Aquatic Sciences*. 209:1-144.
13. POSEY, M. H. 1985. The effects upon the macrofaunal community of a dominant burrowing deposit feeder, *Callianassa californiensis*, and the role of predation in determining its intertidal distribution. Ph.D. University of Oregon.

Updated 2014

Owenia collaris

A tube-dwelling polychaete worm

Phylum: Annelida
Class: Polychaeta
Order: Oweniida
Family: Oweniidae

Taxonomy: *O. collaris* was originally considered a subspecies of *O. fusiformis* (Hartman in 1955) and was later defined as a valid species by the same author (1969) based on the presence of a thoracic collar. Based on morphological characters, Dauvin and Thiébaud (1994) designated *O. fusiformis* as a cosmopolitan species, considering most *Owenia* species (including *O. collaris*) junior synonyms of *O. fusiformis* while reducing the genus *Owenia* to two species. Character-based and molecular phylogenetics have revealed that *O. fusiformis* is a cryptic species complex (Blake 2000; Ford and Hutchings 2005; Capa et al. 2012) in which *O. collaris* is a distinct species (Blake 2000).

Description

Size: Individuals are moderate sized and up to 54 mm (Blake 2000) in length and 3 mm in width. Although specimens up to 100 mm in length (Berkeley and Berkeley 1952) and tubes up to 90 mm in length (Hartman 1969) have been reported. The specimen upon which the description is based was 27 mm in length and 1.0 mm in width with 18 segments (from Coos Bay).

Color: Buccal membrane (crown) is pale gray green, with white band. Body pale green flushed with pale reds. Preserved specimens are pale with large reddish brown shield pattern running length of first three setigers (Fig. 2a).

General Morphology: Slender and fragile but somewhat rigid with truncated anterior that tapers posteriorly. (Blake 2000).

Body: Body cylindrical with first four anterior segments short, middle segments long and posterior segments short (Fig. 1). Thorax and abdomen not morphologically distinct. 18-28 segments (Dales 1967).

Anterior: Prostomium reduced with no sensory appendages except frilly buccal membrane or tentacular crown.

Prostomium fused with peristomium, forming a collar whose margin is complete except for a pair of ventral lateral notches (Hartman 1969) (Fig. 2b). Mouth is terminal (Blake 2000) and surrounded by three peristomial lips (one dorsal, two ventral) (Fig. 4), which can be used directly for feeding (Dales 1967).

Trunk: Body segments are inconspicuous and only marked by presence of setae. Abdominal groove present and dorsal glandular ridges absent (Blake 2000).

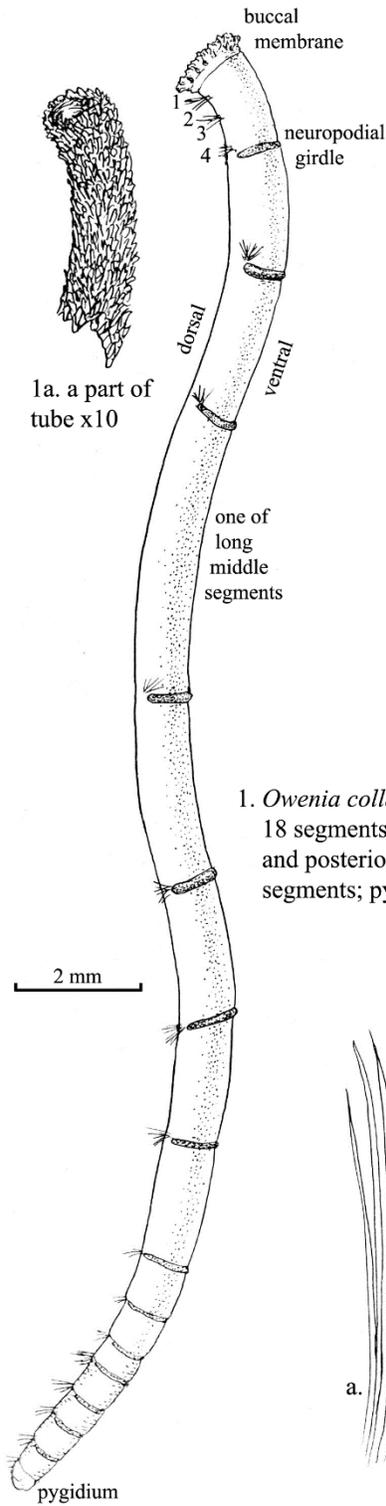
Posterior: Pygidium lobed (10 or more lobes) when expanded, but is usually contracted when collected (Berkeley and Berkeley 1952; Blake 2000) (Fig. 1).

Parapodia: Reduced and biramous both notosetae and neurosetae beginning on setiger four and continuing to posterior. "Neuropodia from setiger four form nearly encircling girdles of closely packed uncini at anterior end of segment" (Hartman 1969) (Figs. 2b, 3b). Each uncinus has a straight stem and 2 teeth (Fig. 3c).

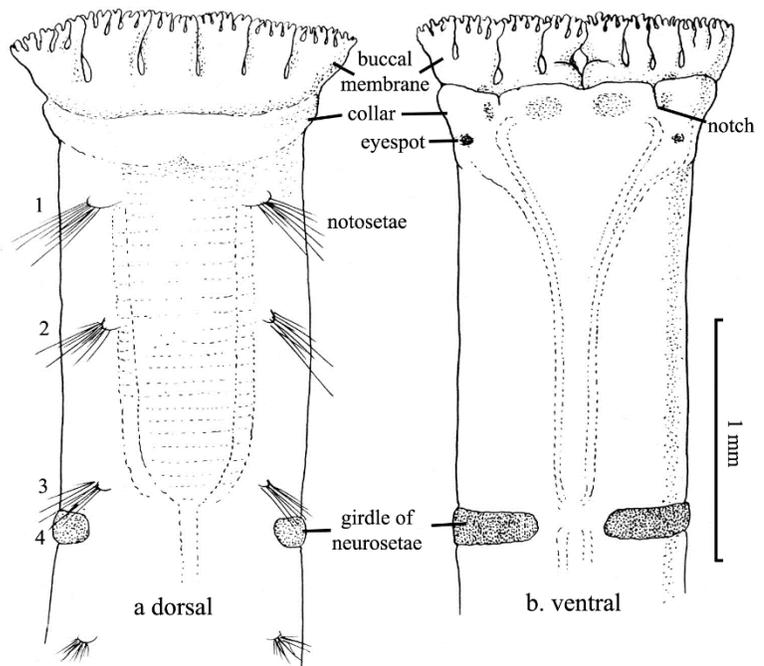
Setae (chaetae): Notosetae consist of serrated capillaries (Blake 2000). First three thoracic setigers have capillary notosetae only (Fig. 2a) (genus *Owenia*). Setiger three is more dorsal and has shorter notosetae (Blake 2000). Abdominal notosetae are thin. Neurosetae are composed of dense small hooks with long shafts (Blake 2000).

Eyes/Eyespots: There is confusion about the presence or absence of peristomial eyes in this species. Two ventral eyes were reported (sp. *collaris*, Hobson and Banse 1981) and observed (Fig. 2b). However, Hartman (1969), Blake (2000) and Blake and Ruff (2007) indicate eyespots are absent.

Owenia collaris

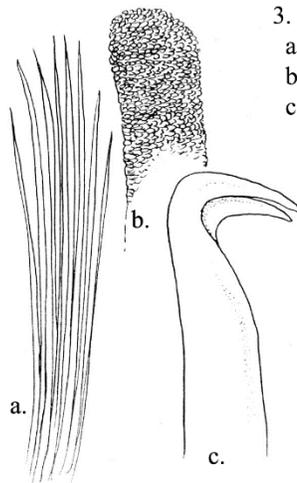


1. *Owenia collaris* (L:27mm) x10:
18 segments; cylindrical, short anterior and posterior segments, long middle segments; pygidium contracted.

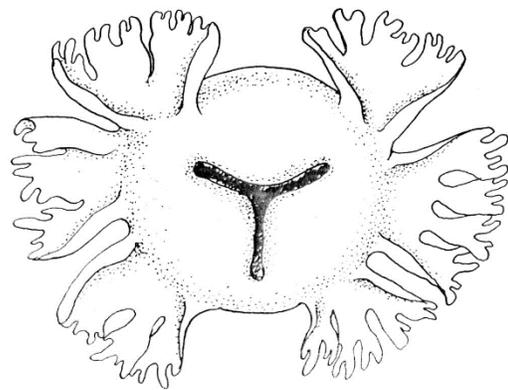


2. Anterior segments x40:
prostomium reduced to a buccal membrane; two ventral eyespots; first three setigers with capillary notosetae only; neurosetal girdles from fourth setiger.

3. Setae:



a. notopodial capillaries (a posterior fascicle) x100
b. part of a neuropodial girdle; uncini closely packed x150
c. uncinus from b. x600



4. Lips, from above x40:
one dorsal, two ventral lobes
(after Watson, 1901).

Anterior Appendages: A buccal membrane at worm anterior forms a crown-like funnel (genus *Owenia*). The crown has 4–10 main branches (eight, Blake 2000) divided into

Branchiae:

Burrow/Tube: Cylindrical or spindle-shaped tube, up to 90 mm long, of overlapping shell fragments and/or sand grains. Each grain is attached at its one end, giving tube a tiled appearance (Fig. 1a). Tube lining is close-fitting, chitinous and tough (genus *Owenia*) and composed of fine filaments secreted by seven pairs of thread glands. Tube grains, usually light-colored, are cemented together by the buccal organ (Watson 1901), concealed by the crown. Tubes taper at both ends.

Pharynx: Bears a proboscis with muscular pad (Fauchald 1977) and pharynx is not eversible (Blake 2000).

Genitalia:

Nephridia:

Possible Misidentifications

Oweniida are all tube dwellers. The Oweniidae is a small family with its own order (Fauchald 1977). It is characterized by its lobed or membranous prostomium fused to the anterior segments. All the anterior segments are long (except the first four in this species) and the posterior segments are short. The neuropodial hooks occur in dense horizontal bands and notosetae are capillary. The prominent buccal membrane of Oweniidae is unique because it is not feathery, or composed of long branchiae, tentacles or of palps. It encircles the entire anterior end of the worm.

Other tube-dwelling polychaete families have buccal tentacles, a crown of radioles or palps, but none has the entire anterior end transformed into a tentacular membrane and thus a greatly reduced prostomium. In addition, oweniids have very short posterior segments with middle and anterior segments long. Other tube-dwelling polychaete families referenced in this guide include: Ampharetidae (see *Hobsonia*

100's of slender tips all of same length (Hartman 1969) (Fig. 2). The membrane functions in respiration and feeding (Dales 1967).

florida), Sabellidae (see *Eudistylia vancouveri*), Terebellidae (see *Pista pacifica* and *Thelepus crispus*).

There are 4 other genera in the family Oweniidae:

Galathowenia spp. have a prostomium with a midventral cleft surrounded by overlapping ventral membranes but lacks anterior appendages. The type species, *G. africana* was described from South Africa (Dales 1967; Blake 2000), but three undescribed species are reported offshore of California (Blake and Ruff 2007).

Myriowenia spp. are recognizable by having deeply bilobed prostomium, with paired palps and no tentacular crown. Their tubes are loose-fitting and easily torn. *M. californiensis* is reported from offshore central California to Oregon in mixed sediments (Blake and Ruff 2007).

Myriochele spp. have a rounded prostomium, no tentacular crown and no midventral cleft. Like *Owenia*, they have only notosetae in the first two or three setigers. Of the dozen or so species of *Myriochele* worldwide (Hobson and Banse 1981), three species are reported offshore in California. *Myriochele striolata* is the only species known in nearshore sediments (Blake and Ruff 2007). This species is distinct in its small size (7–8 mm in length, <1 mm in width and 16–17 setigers) (Blake 2000).

Myrioglobula sp. also have a rounded prostomium and no crown of tentacles, however the first setiger has only notosetae, but no species in this genus are currently reported locally (Blake and Ruff 2007)

The genus *Owenia*, is characterized by its tentacular crown, its lack of neurosetae on the first three setigers, and its close-fitting, firm tube (Fauchald 1977).

Owenia fusiformis differs from *O. collaris* as the latter species has a collar (=collaris), anteriorly (Hartman 1969). *Owenia johnsoni* has much less anterior pigment than *O. collaris*. Additionally, the tentacular crown of *O. collaris* is shorter and bears fewer main branches than *O. johnsoni*. The posterior end is grooved in *O. collaris*, unlike *O. johnsoni* (Blake 2000).

Ecological Information

Range: Type locality is Santa Catalina Island (Hartman 1969). Cosmopolitan distributions previously reported (Berkeley and Berkeley 1952) are likely that of *O. fusiformis*. Blake (2000) suggests that *O. collaris* is found offshore in southern and central CA and this species is also reported in OR (Blake and Ruff 2007).

Local Distribution: In Coos Bay including South Slough and bay mouth. Also Yaquina Bay.

Habitat: Forms large, dense colonies in mud and silty estuarine habitats, but can also be found offshore in sandy sediments (Blake 2000). Found in clean sand and among eel grass roots in Coos Bay.

Salinity: Found at salinities of 30.

Temperature:

Tidal Level: Intertidal and subtidal (to 150 m, Blake 2000).

Associates:

Abundance:

Life-History Information

Reproduction: The reproduction and larval development have been described by Smart and von Dassow (2009). Dioecious and iteroparous, gametes are loose in the coelom (Smart and von Dassow 2009) in males and females which spawn March through September (Washington and Oregon) (Smart et al. 2012). Colorless eggs (70–80 μm) and sperm (4 μm) are released through paired pores in the worm posterior. Once fertilized, cleavage is spiral, gastrulation occurs at 8–9 hours, embryos are ciliated and swimming at 24 hr and develop through trochophores to mitraria larvae (12° C, Smart and von Dassow 2009).

Larva: Planktotrophic mitraria larvae are characterized by triangular bodies with

undulating ciliated margins (Crumrine 2001; Pernet et al. 2002), have two red eyes and are recognizable by two extremely long bundles of chaete, which develop from individual chaetal sacs. These chaetae extend when the larva is disturbed (Fernald et al. 1987). A juvenile rudiment develops after four weeks (12° C). At metamorphosis, the larval body is resorbed into the collar of the juvenile worm (Smart and von Dassow 2009). **Juvenile:** Post-metamorphosis juvenile *O. collaris* are approximately 800 μm in length and have a prostomium and peristomium.

The juvenile has 7–8 segments bearing 1–2 sets of chaetae, a pygidium and begins assembling a tube rapidly. They grow anterior tentacles and reach 1300 μm in length after 24 days (Smart and von Dassow 2009).

Longevity:

Growth Rate:

Food: Both a filter and a surface deposit feeder, picking up particles directly with the lips and selecting particles for size and composition (Fauchald and Jumars 1979). Juveniles are surface deposit feeders at two weeks of age (Smart and von Dassow 2009).

Predators:

Behavior: Individuals can move freely within the tube (Fauchald 1977; Watson 1901).

Bibliography

1. BERKELEY, E., and C. BERKELEY. 1952. Annelid. Polychaeta Sedentaria. Canadian Pacific Fauna. 9b:1-139.
2. 2000b. Family Oweniidae, p. 97-127. *In:* Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel. Vol. 7. J. A. Blake, B. Hilbig, and P. V. Scotts (eds.). Santa Barbara Museum of Natural History, Santa Barbara, California.
3. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In:* Light and Smith manual: intertidal invertebrates from central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.
4. CAPA, M., J. PARAPAR, and P. HUTCHINGS. 2012. Phylogeny of Oweniidae (Polychaeta) based on

- morphological data and taxonomic revision of Australian fauna. *Zoological Journal of the Linnean Society*. 166:236-278.
5. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 6. DALES, R. P. 1967. *Annelids*. Hutchinson & Co., Ltd., London.
 7. DAUVIN, J.-C., and E. THIÉBAUT. 1994. Is *Owenia fusiformis* Delle Chiaje a cosmopolitan species? *Mémoires du Muséum national d'histoire naturelle*. 162:383-404.
 8. FAUCHALD, K. 1977. The Polychaete worms: definitions and keys to the orders, families and genera. Natural History Museum of Los Angeles County, Los Angeles.
 9. FAUCHALD, K., and P. A. JUMARS. 1979. Diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology*. 17:193-284.
 10. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 11. FORD, E., and P. HUTCHINGS. 2005. An analysis of morphological characters of *Owenia* useful to distinguish species: description of three new species of *Owenia* (Oweniidae: Polychaeta) from Australian waters. *Marine Ecology*. 26:181-196.
 12. HARTMAN, O. 1969. Atlas of the sedentariate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
 13. HOBSON, K. D., and K. BANSE. 1981. Sedentariate and archiannelid polychaetes of British Columbia and Washington. *Canadian Bulletin of Fisheries and Aquatic Sciences*. 209:1-144.
 14. PERNET, B., P. Y. QIAN, G. ROUSE, C. M. YOUNG, and K. J. ECKELBARGER. 2002. Phylum Annelida: Polychaeta. *In: Atlas of marine invertebrate larvae*. C. M. Young, M. A. Sewell, and M. E. Rice (eds.). Academic Press, San Diego, CA.
 15. SMART, T. I., and G. VON DASSOW. 2009. Unusual development of the mitraria larva in the polychaete *Owenia collaris*. *Biological Bulletin*. 217:253-268.
 16. SMART, T. I., C. M. YOUNG, and R. B. EMLET. 2012. Environmental cues and seasonal reproduction in a temperate estuary: a case study of *Owenia collaris* (Annelida: Polychaeta, Oweniidae). *Marine Ecology*. 33:290-301.
 17. WATSON, A. T. 1901. On the structure and habits of the Polychaeta of the family Ammocharidae. *Journal of the Linnean Society of London, Zoology*. 28:230-260.

Updated 2014

Glycera robusta

The large proboscis worm

Phylum: Annelida
Class: Polychaeta
Order: Phyllodocida
Family: Glyceridae

Taxonomy: There are relatively few glycerid genera and *Glycera* contains the largest number of species. Several authors have attempted to divide this genus into subgenera or genera. Groups have been divided based on proboscideal organs (but no formal genera designated) by Hartman (1950) and recent reviews have synonymized species (Böggemann 2002) or split the genus into many sibling species (e.g. O'Connor 1987). *Glycera robusta*, however, is unique in its universal stability as a valid taxon with a reliable description (Scamit 2002; Blake and Ruff 2007).

Description

Size: The largest of the Glyceridae, up to 800 mm in length and 22 mm in width (Berkeley and Berkeley 1942; Hilbig 1997) and can have up to 300 segments (Hartman 1968). The illustrated specimen, from South Slough of Coos Bay, was 500 mm in length and 20 mm in width.

Color: Dark red, but can be yellow-brown. Their color gives rise to the common name of the family Glyceridae – the blood worms (Blake and Ruff 2007).

General Morphology: Long, stout and stiff worms with numerous densely packed segments and a conical and annulated anterior that tapers to a point (Glyceridae, Blake and Ruff 2007). *Glycera robusta* is dorsoventrally flattened in cross-section, is widest in anterior regions, and gradually tapers to a point posteriorly (Hilbig 1997) (Fig. 1).

Body: Members of the family Glyceridae lack a separate circulatory system and their coelomic fluid contains hemoglobin (Terwilliger et al. 1976; Morris et al. 1980) that is visible through the thin body wall. Unlike other glycerids, *Glycera robusta* contains both coelomic cell hemoglobin and myoglobin within the body wall musculature (Terwilliger and Garlick 1978).

Anterior: Glycerids are characterized by their conical,

annulated and elongate prostomia that taper to a fine point anteriorly (Blake and Ruff 2007). The prostomium is small and bears 10 biannulate rings, the first being approximately one third of the total length (Fig. 2). The prostomium is longer than it is wide (Hilbig 1997) (Fig. 2) and the basal prostomial ring is fused with the peristomium (Blake and Ruff 2007).

Trunk: Segments posterior to peristomium are considerably wider than anterior most segments (Hilbig 1997) (Fig. 2). The body bears numerous, tightly packed segments.

Posterior: Anal end is narrow and tapers to a fine point, adorned with a pair of small cirri (Fig. 1) (Berkeley and Berkeley 1942).

Parapodia: Inconspicuous, biramous (Fig. 4) and one-tenth of total body width in mid-body regions (Hilbig 1997). Pre- and post-acicular lobes are equally bifid, the former resembling the ventral cirrus (Fig. 4) (Blake 1975) while the post-acicular lobes are short (Hartman 1968). The dorsal parapodial margin with blister-like, fleshy branchia (see **Branchiae** below) (Fig. 4).

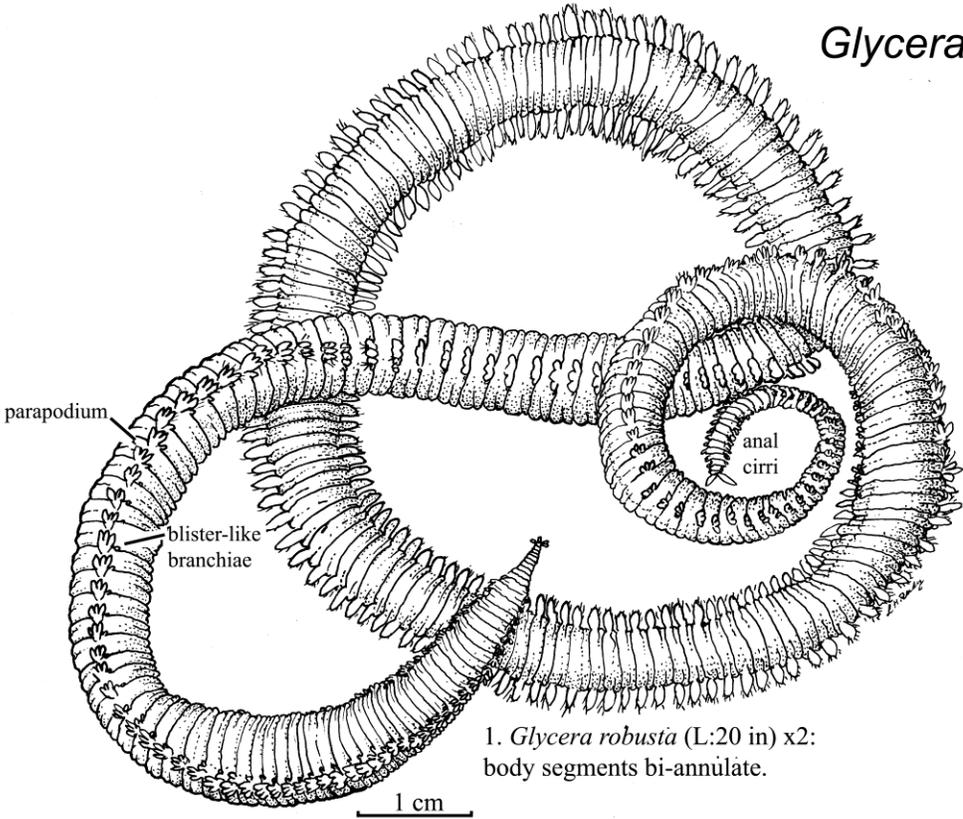
Setae (chaetae): Notosetae simple, slender and finely serrated capillaries and neurosetae are compound spinigers that are slightly wider than notosetae (Hilbig 1997) (Fig. 5).

Eyes/Eyespots: No eyespots are visible, although small eyespots may be present on the terminal prostomial ring (Glyceridae, Blake and Ruff 2007).

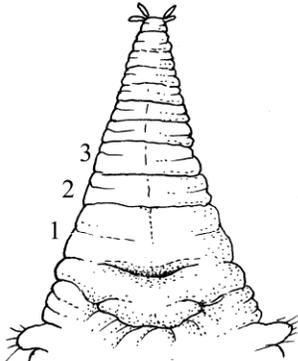
Anterior Appendages: The anteriormost prostomial ring bears two pairs of small and bifurcate terminal cirri, but no other anterior appendages are present (Blake and Ruff 2007) (Fig. 2).

Branchiae: Blister-like branchiae begin on setiger 23 (Fig. 1, 4). The branchiae protrude from dorsal parapodial walls from setiger 23–34 and (in large specimens) branchiae are present along the ventral parapodial walls beyond setiger 35 (Hilbig 1997). The

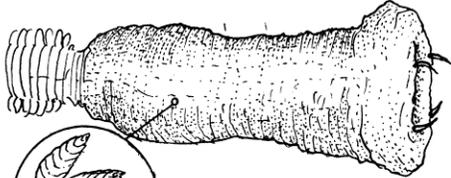
Glycera robusta



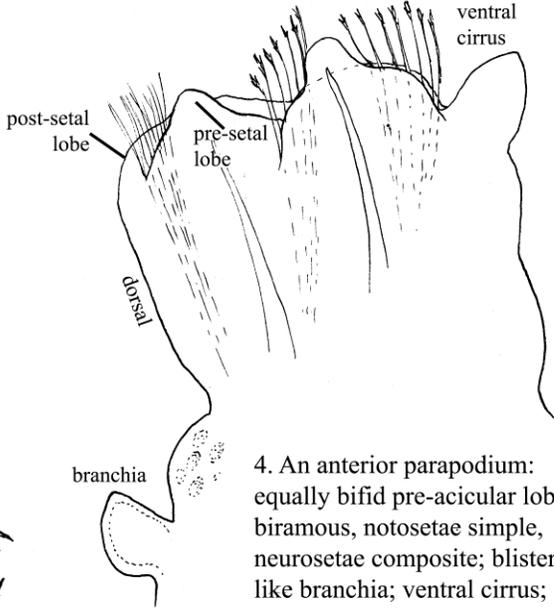
1. *Glycera robusta* (L:20 in) x2:
body segments bi-annulate.



2. Prostomium:
ten bi-annulate rings, four
small terminal cirri.



3. Proboscis:
everted, four terminal black
jaws, simple surface papillae.



4. An anterior parapodium:
equally bifid pre-acicular lobes;
biramous, notosetae simple,
neurosetae composite; blister-
like branchia; ventral cirrus;
two post-setal lobes.



5. Composite neuroseta.

presence of branchiae ventrally and dorsally was once thought to be characteristics of different species, but was found to be a character that varies with individual size (Berkeley and Berkeley 1942; Hilbig 1997).

Burrow/Tube:

Pharynx: Bears large and powerful proboscis (up to 26 mm long) (Hartman 1968). When fully everted, four terminal black chitinous jaws are visible, each jaw composed of a hook-like fang and a V-shaped support (called an aileron). The ailerons in *G. robusta* consist of a thick outer ramus and a very thin inner ramus (Hilbig 1997). The proboscis epithelium is densely covered with pear-shaped papillae, called proboscideal organs (Berkeley and Berkeley 1942; Blake and Ruff 2007) (Fig. 3). These proboscideal organs are oval to flask shaped, bearing 6–8 ridges (Hilbig 1997) (Fig. 3).

Genitalia:

Nephridia:

Possible Misidentifications

Distinctive characters of the Glyceridae include a pointed and annulated prostomium with two pairs of anterior appendages and a long, powerful proboscis with four hook-shaped jaws and accessory ailerons (Böggemann et al. 2012). The other proboscis worm family, the Goniadidae, is morphologically similar to the Glyceridae and identification requires examination of the parapodia and proboscis. The Goniadidae have bodies divided into three parts by different types of parapodia and their bodies are usually more cylindrical and slender than is seen in the Glyceridae (Hilbig 1997; Blake and Ruff 2007). The everted proboscis of goniadids also have two jaws, not four, and a row of denticles (called chevrons, Böggemann et al. 2012). The genus *Glycera* is characterized by its pointed and annulated prostomium, four small anterior cirri, peristomium fused to basal prostomial rings, a cylindrical proboscis with proboscideal organs and four fang-like jaws terminally (Hilbig 1997). Members of this genus also have biramous parapodia with two pre-setal and 1–2 post-setal lobes, short dorsal cirri and elongate ventral cirri. They usually have branchiae, simple notosetae and compound neurosetae. There are currently

five local *Glycera* species (Blake and Ruff 2007).

G. americana, with four-lobed parapodia and branched, retractile branchiae (Hartman and Reish 1950), is found intertidally to 120 m. *G. nana* (= *capitata*), another large species (but only up to 100 mm), with two pre-setal parapodial lobes, and one post-setal lobe, but no branchiae. *G. macrobranchia* (= *convoluta*) has a single non-retractile branchia and 14 to 16 annulations in the prostomium (unlike 10 in *G. robusta*). *G. dibranchiata* has two finger-like branchiae, one above and one below the setal lobe, this species is commonly harvested for bait in Canada and along the eastern coast of the United States. *G. tenuis* has but one pre-setal parapodial lobe on its posterior setiger, is only 80 mm in length, when mature, and 13–16 proboscideal organs (Blake and Ruff 2007).

Ecological Information

Range: Type locality is California (Hartman 1968). Known range includes the western (Japan) and eastern Pacific (Washington to southern California), however, *G. robusta* is not currently in Puget Sound Keys (e.g. Kozloff 1974).

Local Distribution: Coos Bay distribution includes many sites in the bay, such as South Slough and Fossil Point, and outside the bay, in the small sandy beaches at Cape Arago (Hartman and Reish 1950).

Habitat: *Glycera robusta* preferred substrates include beds of black mud (Ricketts and Calvin 1971), gravelly sand (Hartman 1968), and sand and cobble sediments (Blake and Ruff 2007).

Salinity:

Temperature:

Tidal Level: Intertidal and shelf depths (Hartman 1968; Blake and Ruff 2007).

Associates:

Abundance:

Life-History Information

Reproduction: The reproduction and development of *G. robusta* is not known. Most glycerids become epitokous in spring and summer months (Morris et al. 1980) and females release lens-shaped oocytes (Fernald et al. 1987).

Larva: Development proceeds via an eyeless trochophore larva. These planktotrophic larvae feed on diatoms and detritus, eventually developing to epibenthic stages and become predatory once their jaws are fully formed (Fernald et al. 1987). Many of the locally known *Glycera* species produce nectochaete larvae that are characterized by a long, pointed and annulated prostomium as is seen in the adults (Fig. 14, Crumrine 2001).

Juvenile:

Longevity:

Growth Rate:

Food: Glycerids are mainly carnivorous (Crumrine 2001).

Predators:

Behavior: Individuals use their proboscis to burrow quickly.

Bibliography

1. BERKELEY, E., and C. BERKELEY. 1942. North Pacific Polychaeta, chiefly from the west coast of Vancouver Island, Alaska, and Bering Sea. *Canadian Journal of Research*. 20:183-208.
2. BLAKE, J. A. 1975. Phylum Annelida: Class Polychaeta, p. 151-243. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
3. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In: The Light and Smith manual: intertidal invertebrates from California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
4. BOEGGEMANN, M. 2002. Revision of the Glyceridae GRUBE 1850 (Annelida: Polychaeta). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*:1-249.
5. BOEGGEMANN, M., C. BIENHOLD, and S. M. GAUDRON. 2012. A new species of Glyceridae (Annelida: 'Polychaeta') recovered from organic substrate experiments at cold seeps in the eastern Mediterranean Sea. *Marine Biodiversity*. 42:47-54.
6. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
7. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
8. HADERLIE, E. C. 1980. Polychaeta: the marine annelid worms, p. 448-489. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
9. HARTMAN, O. 1968. Atlas of the Errantiate Polychaetous Annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
10. HARTMAN, O., and D. J. REISH. 1950a. Goniadidae, Glyceridae and Nephtyidae. *Allan Hancock Pacific Expedition*. 15:1-182.
11. —. 1950b. The marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
12. HILBIG, B. 1997. Family Glyceridae, p. 187-205. *In: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel*. Vol. 4. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
13. KOZLOFF, E. N. 1974. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago and adjacent regions. University of Washington Press, Seattle and London.
14. O'CONNOR, B. D. S. 1987. Glyceridae (Polychaeta) of the North Atlantic and Mediterranean, with descriptions of two new species. *Journal of Natural History*. 21:167-189.
15. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.

16. SCAMIT. 2002. Minutes of the 21 October Meeting. SCAMIT Newsletter. 27:1-6.
17. TERWILLIGER, R. C., and R. L. GARLICK. 1978. Hemoglobins of *Glycera robusta*: oxygen equilibrium properties of celomic cell hemoglobin and body wall myoglobin. Comparative Biochemistry and Physiology Part A. 59:359-362.
18. TERWILLIGER, R. C., R. L. GARLICK, and N. B. TERWILLIGER. 1976. Hemoglobins of *Glycera robusta*: structures of coelomic cell hemoglobin and body wall myoglobin. Comparative Biochemistry and Physiology Part B. 54:149-153.

Updated 2015

Glycinde armigera

A proboscis worm

Phylum: Annelida
Class: Polychaeta
Order: Phyllodocida
Family: Goniadidae

Description

Size: Individuals reaches lengths up to 118 mm and widths of 3 mm (Hilbig 1997). The illustrated specimen 30 mm in length.

Color: Pale orange, slightly iridescent, often with transverse pigment bands on each segment. Alcohol preserved specimens are pale yellow (Hilbig 1997).

General Morphology: Small, slender worms are recognizable by a long, conical annulated prostomium (Goniadidae, Blake and Ruff 2007).

Body: The body of goniadids is divided into three distinct regions (Blake and Ruff 2007). There are 100–144 total body segments in *G. armigera* which are broken up as follows: 1) anterior region, devoid of gametes, comprising 27–30 segments with uniramous parapodia (Fig. 4a); 2) a transitional area of 47+ segments where notopodia gradually develop; 3) a posterior area, where gametes can be observed with 25–60 segments having biramous parapodia (Fig. 4a) (Hilbig 1997).

Anterior: Prostomium is fused with peristomium and is much longer than wide, cone-shaped and annular with eight to nine annulations (rings) (Fig 2).

Trunk:

Posterior: Pygidium bears a pair of anal cirri that can be very long and filiform (Hilbig 1997), but were rather short and stubby in the illustrated specimen.

Parapodia: Uniramous in anterior setigers, but biramous from setiger 30. Parapodia are long and conspicuous. Both dorsal and ventral cirri are conical to fingerlike and are larger than neuropodial lobes anteriorly (Hilbig 1997). Dorsal cirri are not incised. Pre-setal lobes of twenty-fifth parapodia are heart-shaped (Fig. 4a).

Setae (chaetae): Neurosetae are slender and compound spinigers have shafts that are smooth and with serrated blades. Notosetae are small, long, and serrated distally (see Hilbig 1997 Fig. 7.1P-Q).

Eyes/Eyespots: A pair of eyes exists at the base of prostomial annulations (*Glycinde*, Hilbig 1997).

Anterior Appendages: Four small and biarticulate antennae occur at the anteriormost tip of prostomium.

Branchiae:

Burrow/Tube:

Pharynx: Pharynx bears a very long proboscis (reaching to setiger 50) which is large and powerful when everted (*Glycinde*, Blake 1975; Hilbig 1997). The everted proboscis surface is densely covered in proboscideal organs, and large, chitinized spines, a circle of denticles and two large toothed jaws with three to four teeth each (Hilbig 1997; Smith et al. 1995) (Fig. 3). The arrangement of the various proboscideal organs is taxonomically significant and their distribution is divided into five regions along the proboscis (Hartman and Reish 1950; Fig. 1, Smith et al. 1995).

Genitalia:

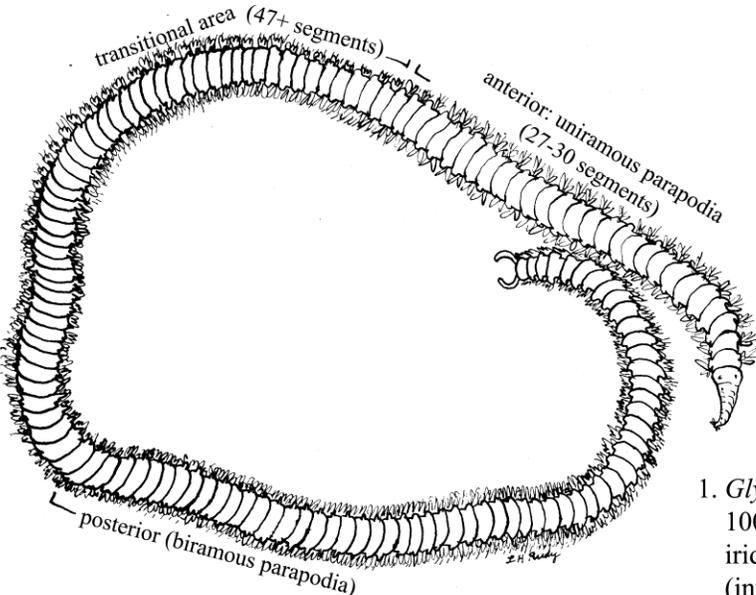
Nephridia:

Possible Misidentifications

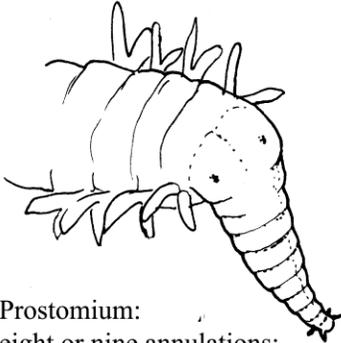
Members of the family Goniadidae are distinguished from those of the similar family Glyceridae by the lack of distinct body regions in glycerids and species that more readily evert their proboscis among the later family. Further examination of proboscis armature is necessary to differentiate species in these families (Blake and Ruff 2007). The genus *Glycinde* is characterized by a pointed and annulated prostomium, four small anterior antennae, a pair of eyes, and a large proboscis that is armed with a circlet of jaws (Hilbig 1997).

There is only one other co-occurring species in this genus reported from central California to Oregon, *G. picta* (= *G. polygnatha*) (Blake and Ruff 2007). The proboscis armature forms a ventral

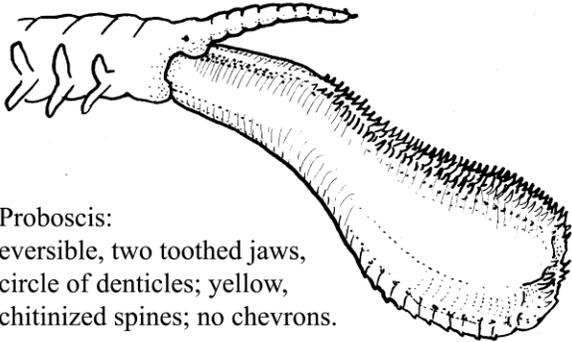
Glycinde armigera



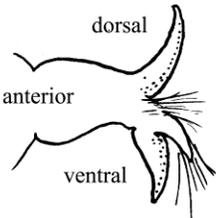
1. *Glycinde armigera* (L:3cm) x15:
100-144 segments; pale orange, slightly iridescent, darker under parapodia (interior blood).



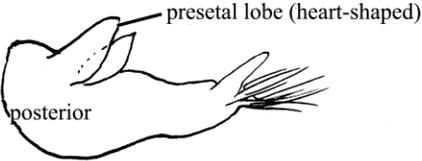
2. Prostomium:
eight or nine annulations;
basal eyes (distal not shown).



3. Proboscis:
eversible, two toothed jaws,
circle of denticles; yellow,
chitinized spines; no chevrons.



4a. Parapodia:
dorsal and ventral cirri conical,
dorsal cirri not incised.



4b. Doral cirrus:
G. polygnatha, anterior,
dorsal incised.

arc in this species that is lacking in *G. armigera* (Hilbig 1997). Furthermore, the anterior dorsal cirri of *G. picta* are incised (Fig. 4b), and the shape of the papillae differs between the two species (in region five, see plate 154 Blake and Ruff 2007), duck-foot shaped in *G. picta* and conical in *G. armigera*. *Glycinde picta*, from British Columbia, Canada has pre-setal lobes which narrow distally (after the 25th parapodia), but are not heart-shaped. Another similar goniadid polychaete is *Goniada brunnea*, a large (up to 160 mm in length), dark brown species, with distinct chevrons on the sides of the proboscis (Hilbig 1997).

Ecological Information

Range: Type locality is southern California. Known range includes western Canada to Panama and the Galapagos Islands (Hilbig 1997).

Local Distribution: Coos Bay sites include South Slough, both intertidally and dredged from stations 1–6 (see Porch 1970). Oregon distribution includes sites in Reedsport and Depoe Bay to depths up to 135 m (Hartman and Reish 1950).

Habitat: Intertidal in muddy and mixed sand flats and amongst eelgrass (Hartman 1968).

Salinity:

Temperature:

Tidal Level: Low intertidal to 1100 m (Hilbig 1997).

Associates: Other polychaetes, amphipods, grass shrimp, barnacles.

Abundance: Widespread distribution, but low abundance in Coos Bay (Porch 1970).

Life-History Information

Reproduction: Epitokous from October through February (Hilbig 1997) and, although sexually mature adults have not been observed, larvae were most abundant in plankton samples taken in Tomales Bay, CA from February through April (in 1972, Blake 1975).

Larva: The larvae of *G. armigera* were described from wild-caught individuals by

Blake (1975). Trochophore larvae are nearly as wide as they are long (330 μm in length and 270 μm in width), they have a prototroch with long and short cilia and a neurotroch, extending from the mouth to the anal pore. Additionally, trochophore larvae can be recognized by green pigment near the prototroch and anal regions (Fig. 24A-B, Blake 1975). This green pigment is also apparent in the metatrochophore stage, but is distributed more generally throughout the entire body, with concentrated regions near the prototroch, lateral edges of segments and pygidium. Eventually, a deep red pigment develops in the intestine (Crumrine 2001). Metatrochophores bear setae, have a broad prostomium, distinct prototroch of long cilia with two red eyes anterior to the prototroch. The pygidium at this stage has a pair of anal cirri (Fig. 24C, Blake 1975). By the nectochaete stage, the prostomium resembles the pointed shape with annulations seen in adult *G. armigera* and has four frontal antennae. As the larva grows into a late nectochaete stage, the pharynx, proboscis and proboscis armature become fully developed when the larva is approximately 1200 μm in length (Fig. 24D, Blake 1975).

Juvenile: Post-larval settlement densities were highest in April through May reaching 513 individuals/ m^2 in April. Rates of post-larval settlement ranged from 20.4–24.5 individuals/ m^2/day (Kudenov 1979).

Longevity:

Growth Rate:

Food:

Predators:

Behavior: A very active species where the large proboscis is used in burrowing and feeding.

Bibliography

1. BLAKE, J. A. 1975. The larval development of Polychaeta from the northern California coast. III. Eighteen species of Errantia. *Ophelia*. 14:23-84.

2. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In*: Light and Smith manual: intertidal invertebrates from central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.
3. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
4. HARTMAN, O. 1968. Atlas of the Errantiate Polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
5. HARTMAN, O., and D. J. REISH. 1950. The marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
6. HILBIG, B. 1997. Family Goniadidae, p. 109-178. *In*: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel. Vol. 4, The Annelida, Part 2. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara.
7. KUDENOV, J. D. 1979. Post-larval polychaetes in sandy beaches of Tomales Bay, California. Bulletin of the Southern California Academy of Sciences. 78:144-147.
8. PORCH, L. L. 1970. Polychaetes of Coos Bay. *In*: OIMB Unpublished Student Report, Summer 1970.
9. SMITH, L. E., S. TRABANINO, and R. J. BAERWALD. 1995. Scanning electron-microscopic observations of the proboscideal papillae of *Glycinde armigera* (Annelida, Polychaeta). Invertebrate Biology. 114:46-50.

Updated 2015

Scoletoma zonata

Phylum: Annelida
Class: Polychaeta
Order: Phyllodocida
Family: Lumbrineridae

Taxonomy: Classifying lumbrinerids is notoriously difficult at the generic level (Blake and Ruff 2007). Most recently, *Scoletoma zonata* was a member of the genus *Lumbrineris*, one that many authors have attempted to divide due to incomplete descriptions and lack of type material. Frame (1992) designated genera based on setal morphology: species with composite hooks, simple hooks and simple limbate setae fall within *Lumbrineris* and those with simple hooks and simple limbate setae fall within *Scoletoma* (Frame 1992). Thus, *S. zonata* is the name currently used (Blake and Ruff 2007).

Description

Size: Individuals often large, exceeding 200 mm (Kozloff 1974) with average sizes 160–200 mm in length and 4.5 mm in width (Hartman 1968). The illustrated specimen (from South Slough) was 160 mm long.

Color: Light red orange to bronze and highly iridescent.

General Morphology: Long, cylindrical worms with a relatively featureless anterior (Lumbrineridae, Blake and Ruff 2007).

Body: Body smooth, elongated, cylindrical and earthworm-like (Ricketts and Calvin 1971) with no ventral groove (Fig. 1). Body segments total more than 200. First two body segments are achaetous and apodous.

Anterior: Prostomium simple, bluntly conical, with no appendages (Fig. 2) (*Scoletoma*, Hilbig 1993).

Trunk:

Posterior: Pygidium gradually tapers to a point, no appendages (Fig. 1).

Parapodia: Small and uniramous. Anterior postsetal lobes shorter than presetal lobes (Fig. 3). Posterior parapodia have postsetal lobes only slightly longer than presetal.

Setae (chaetae): Anterior parapodia with limbate setae and simple falcigers or hooks (Fig. 3). Posterior parapodia with simple falcigers, with multidentate tips, and yellow acicula (Fig. 4a, 4b).

Eyes/Eyespots: No eyes (Lumbrineridae, Blake and Ruff 2007).

Anterior Appendages: None.

Branchiae: None.

Burrow/Tube: An active burrower, *S. zonata* does not build permanent burrow.

Pharynx: The jaw (maxillary) morphology has become useful in lumbrinerid taxonomy, but the pharynx must be dissected to observe them. In *Scoletoma* species, the maxillary apparatus is composed of five pairs of maxillae: maxillae I and II are of equal length and I is without accessory teeth and with attachment lamellae, while II has wide attachment lamellae long the posterior edge. Maxillae III and IV also have a wide attachment lamellae and are pigmented. The final maxillae (V) are free and lateral to IV and III (Carrera-Parra 2006).

Genitalia:

Nephridia:

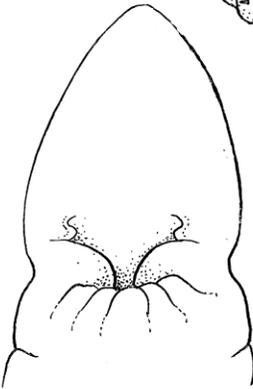
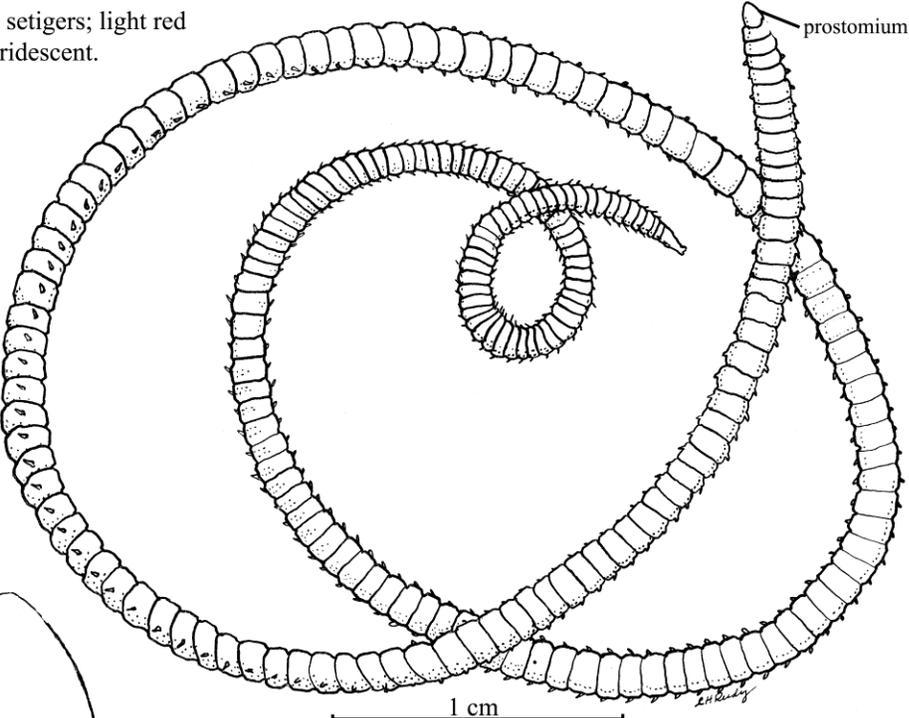
Possible Misidentifications

The family Lumbrineridae is composed of burrowing worms with relatively simple morphology, making taxonomy at the generic level difficult and resulting in many revisions over time. There are currently nine species from three genera reported from central California to Oregon (Blake and Ruff 2007). The three genera are *Eranno*, *Lumbrineris* and *Scoletoma*. Current taxonomy of these genera includes characters of maxillary (jaws) or setal morphology. Members of the genus *Eranno*, for example, have setae that include limbate capillaries and simple hooks, but they can also be recognized by a support plate between maxillae I and II (Frame 1992; Hilbig 1993). *Lumbrineris* species have simple limbate capillaries and hooks as well as composite hooded hooks, where *Scoletoma* does not have composite hooded hooks.

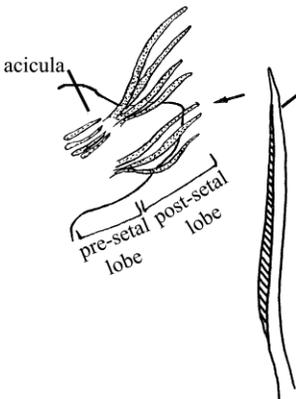
Lumbrineris currently includes five local species. *L. californiensis*, *L. japonica* and *L. inflata* can be differentiated by the

Scoletoma zonata

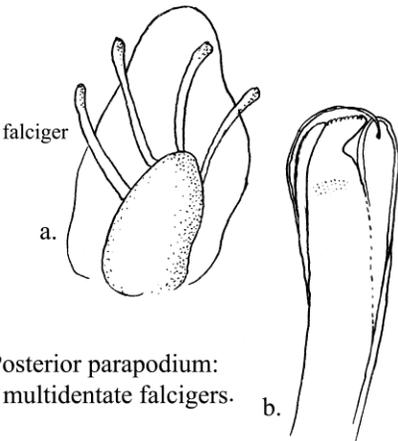
1. *Scoletoma zonata* 5x:
over 200 setigers; light red
orange, iridescent.



2. Prostomium (ventral view):
bluntly conical, eyeless; first two
segments no setae or parapodia.



3. Anterior parapodium:
no branchiae, short post-setal
lobes.



4a. Posterior parapodium:
with multidentate falcigers.

4b. Simple falciger, enlarged.
(Hartman 1968, p. 777)

shape of their prostomium (Plate 160, Blake and Ruff 2007). *L. latreilli*, a cosmopolitan species, is pale red to brown has yellow acicula. *L. japonica*, a rare species, is reddish-brown and iridescent, and with black acicula. *L. cruzensis*, a subtidal species, is recognizable by a single tooth on each maxilla III and IV (Blake and Ruff 2007).

Three species of *Scoletoma* occur locally. *S. erecta* with long posterior postsetal lobes that stand erect and are iridescent bronze in color. *S. luti* (= *L. luti*) with yellow acicula, is very small (under 50 mm) and has very long posterior postsetal lobes (Hartman 1968; Blake and Ruff 2007).

Ecological Information

Range: Type locality is Salmon Bay, Puget Sound, Washington. Known range Alaska to western Mexico (Hartman 1968).

Local Distribution: Coos Bay estuaries and mudflats (e.g. Metcalf mudflat, South Slough) and outer coast, also common in Puget Sound (Kozloff 1974).

Habitat: Substrate includes mud and chips and eelgrass areas (Porch 1970). Intertidally in mud, under rocks and amongst mussel and barnacle beds. Along the outer coast individuals occur among holdfasts and in mudflats of protected areas (Ricketts and Calvin 1971). **Salinity:** Found in in salinity from 10 to 30 in Coos Bay.

Temperature: Collected at temperatures from 8–18°C in Coos Bay.

Tidal Level: High intermediate intertidal to 84 m depths.

Associates: Associates include other polychaetes (e.g. *Abarenicola*), amphipods and tanaidaceans.

Abundance: The most common lumbrinerid in northern California and in the intertidal northeast Pacific (Hartman 1944; Ricketts and Calvin 1971). Also common in Coos Bay (Porch 1970).

Life-History Information

Reproduction: Eggs approximately 500 µm in diameter. In California, development occurs in February (Hartman 1939 in Richards 1967).

Larva: Development is direct and adults brood larvae (Crumrine 2001) and 3-setiger stage larvae have been found along the walls

of adult burrows in summer months (Washington, Fernald et al. 1987).

Juvenile:

Longevity:

Growth Rate:

Food: Ingests mud and eats detritus. No animal remains were observed in the guts of *Scoletoma* sp. (Banse and Hobson 1968).

Predators:

Behavior:

Bibliography

1. BANSE, K., and K. D. HOBSON. 1968. Benthic polychaetes from Puget Sound, Washington with remarks on four other species. Proceedings of the United States National Museum. 125:1-53.
2. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
3. CARRERA-PARRA, L. F. 2006. Phylogenetic analysis of Lumbrineridae Schmarda, 1861 (Annelida: Polychaeta). Zootaxa. 1332:1-36.
4. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
5. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
6. FRAME, A. B. 1992. The Lumbrinerids (Annelida, Polychaeta) collected in two northwestern Atlantic surveys with descriptions of a new genus and two new species. Proceedings of the Biological Society of Washington. 105:185-218.
7. HARTMAN, O. 1944. Polychaetous annelids. Parts V-VIII. Allan Hancock

- Pacific Expeditions. Reports. 10:1-525.
8. —. 1968. Atlas of the Errantiate Polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
 9. HILBIG, B. 1993. Family Lumbrineridae, p. 105-166. *In*: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
 10. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
 11. PORCH, L. L. 1970. Polychaetes of Coos Bay. *In*: OIMB Unpublished Student Report, Summer 1970.
 12. RICHARDS, T. L. 1967. Reproduction and development of polychaete *Stauronereis rudolphi* including a summary of development in superfamily Eunicea. *Marine Biology*. 1:124-133.
 13. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.

Updated 2015

Nephtys caeca

A sand worm

Phylum: Annelida
Class: Polychaeta
Order: Phyllodocida
Family: Nephtyidae

Taxonomy: *Nephtys caeca* is the name used in current local intertidal guides (e.g., Blake and Ruff 2007). One can find several synonyms, however, including variants of the generic spelling (*Nephtys*), subjective synonyms (e.g., *N. margaritacea*, *N. oerstedii* and *N. bononensis*) and species described and later determined to be an earlier developmental stage of *N. caeca* (e.g., *Nephtys nudipes*) (Rainer 1991).

Description

Size: Individuals to 20 cm in length and 10–15 mm in width (Hartman 1968). 90–150 total body segments.

Color: Body color is pale pink and can be light to dark green or brown. No prominent external pigment patterns. The proboscis is iridescent.

General Morphology: Anterior cylindrical in cross-section and becomes slender and rectangular posteriorly (Nephtyidae, Blake and Ruff 2007).

Body: Individuals long, slender and quadrangular in cross-section (Hartman 1968).

Anterior: Prostomium pentagonal, flattened and no pigment pattern (Fig. 2).

Trunk: Thick with widely separated parapodial rami (Fig. 1, 5).

Posterior: Pygidium with very small and hairlike posterior cirrus (Fig. 1).

Parapodia: Fleshy flaps extending laterally from each segment, are biramous and rami are widely separated, densely packed and their setae are fan-shaped (Nephtyidae, Blake and Ruff 2007). Each lobe with a broad and rounded notopodium and a neuropodium. Post-acicular lobes become foliaceous posteriorly (Hartman 1968) (Fig. 5). Bears interramal cirri that are long and recurved between the two parapodial lobes (Figs. 3, 5).

Setae (chaetae): All nephtyid setae are simple and the setae of both rami are of similar morphology. Overall, there are four main types of nephtyid setae including

capillary (e.g., spinose), barred (which are pre-acicular), lyrate and setae with spines (Dnestrovskaya and Jirkov 2011). *Nephtys caeca* has fan-like bunches of neuro- and notosetae on the parapodial lobes. Post-acicular setae (Fig. 5) are long and fine, with single lateral barbs (Fig. 4a) and pre-acicular setae short and with transverse bars (Figs. 4b, 5).

Eyes/Eyespots: None (Fig. 2).

Anterior Appendages: Four small, simple (unforked) antennae (Fig. 2).

Branchiae: The interramal cirri, which are inserted just beneath each dorsal cirrus, are sometimes called branchiae (Blake and Ruff 2007).

Burrow/Tube: *Nephtys caeca* can move rapidly through loose sand and makes temporary burrows (MacGinitie 1935).

Pharynx: Bears short and wide proboscis with a variety of papillae, their number and arrangement is of taxonomic significance (Blake and Ruff 2007). The proboscis in *Nephtys* species can be divided into three distinct regions including the proximal, sub distal and distal (Lovell 1997) (Fig. 1). The proboscis, when fully everted, is globular, with 22 rows of paired distal papillae forming a crown-like structure. Twenty-two rows of sub distal papillae with five small papillae in each row (Fig. 1). The proximal surface of the proboscis is rough and covered with minute wart-like papillae (Fig. 1).

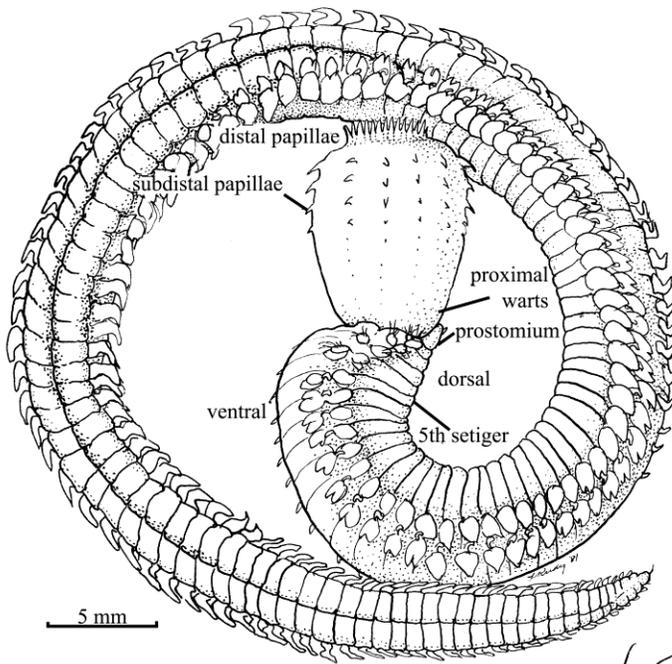
Genitalia:

Nephridia:

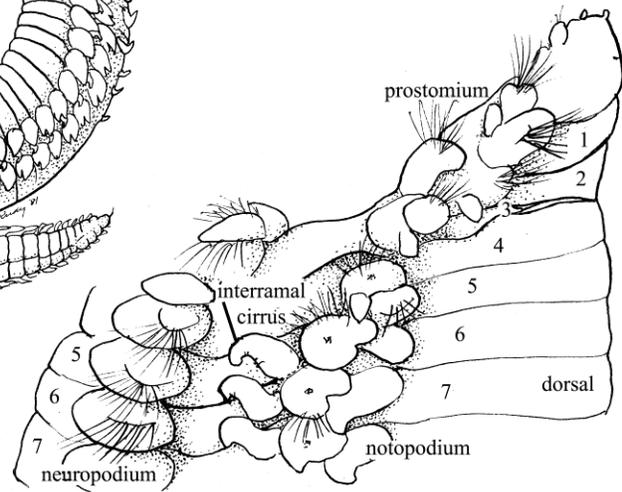
Possible Misidentifications

Worms of the family Nephtyidae can be distinguished by their anteriorly cylindrical and posteriorly rectangular bodies (in cross section), well-developed bi-lobed parapodia, interramal cirri, four small prostomial antennae, and eversible globular proboscis with terminal rows of papillae. They are strong and muscular worms that can be good burrowers and strong swimmers (Blake and Ruff 2007). Nephtyids superficially resemble

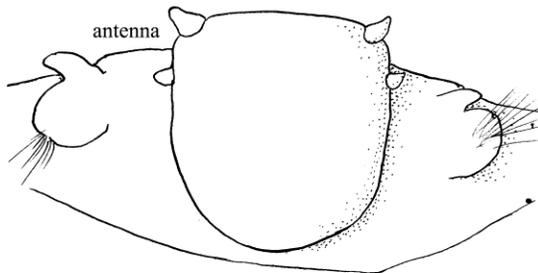
Nephtys caeca



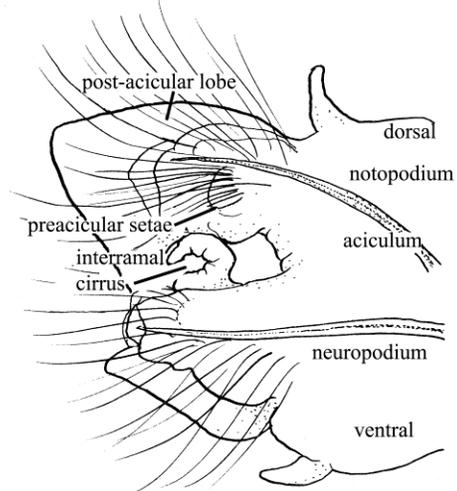
1. *Nephtys caeca* (lateral view) x4: to 150 segments; everted proboscis with 22 rows of distal papillae; subdistal papillae 22 rows of 5; proximal proboscis surface rough; body cross section rectangular.



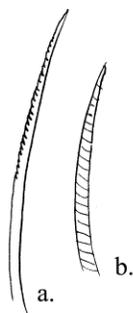
3. Anterior parapodia (lateral view) x30: interramal cirri begin on 5th cirri; parapodia bilobed neuro- and notopodia.



2. Prostomium (dorsal view) x30: pentagonal, eyeless; four small antennae.



5. 90th parapodium x30: biramous; post-acicular lobes large, foliaceous; recurved interramal cirrus beginning on fifth segment; long, fine noto- and neurosetae; shorter, barred pre-acicular notosetae.



4. Setae, tips:
a. long, barbed postacicular seta
b. transversely barred preacicular seta (notopodial).

the genus *Nereis*, however, they have no long anterior appendages (tentacular cirri) and their proboscis armature is quite different (Kozloff 1993). The distinctive taxonomic characters of *N. caeca* include 22 distal paired papillae, 22 rows of sub distal papillae with five papillae per row, no unpaired mid dorsal papilla and interramal cirri beginning on setigers five or six (Blake and Ruff 2007).

Some *Nephtys* species are distinguished from each other by very fine morphological details. The species most closely related to and difficult to differentiate from *N. caeca* include *N. caecoides* and *N. californiensis*. *N. caecoides*, is slightly smaller (on average) than *N. caeca*, with dark bands of color on its anterior end, and a smooth proboscis, not a rough one. *N. caecoides* also has an unpaired medial papilla (not present in *N. caeca*) and interramal cirri beginning on the fourth setigers (rather than the fifth or sixth in *N. caeca*). It is probably the closest species, morphologically, to *N. caeca*, and their two distributions overlap in Coos Bay (Porch 1970). *N. californiensis* is found mostly on the outer coast, or if in bays, only in very clean coarse sand. It has a distinctive V-shaped pigment pattern (sometimes with red spot at center) of pigmentation on the lower end of the prostomium, a smooth proboscis without medial papilla, soft silky flowing setae and interramal cirri beginning on the third setiger.

Three other *Nephtys* species are not so easily confused with *N. caeca*. *N. cornuta*, a small species (less than 15 mm in length) that can be identified by its distinctive bifid ventral and posterior antennae. This species often retains larval eyes on the third setiger, a feature which is usually lost in other closely related species (Blake and Ruff 2007). *N. cornuta* can also be differentiated because it has 18 distal paired papillae (instead of 22 in *N. caeca*) (Lovell 1997). *N. punctata* is much like *N. caeca* in size and form (Hartman 1938), but with interramal cirri beginning on setiger 8–10, and with incised acicular lobes in the anterior parapodia. This species is large and muscular with wide body and short parapodia and is currently only reported in

southern California (Hilbig 1997; Blake and Ruff 2007)

N. parva, colorless except for a dark spot in the middle of its prostomium (Hartman 1968), a smooth proboscis proximally, no medial papilla, eyespots on its third setiger and interramal cirri beginning on the fourth setiger. The type material from this species is suspected to have been miscurated and the holotype appears to be that of *N. cornuta*, while the species description and paratypes match *N. caecoides* more closely. Thus, this species is not a currently valid taxon (Lovell 1997; Blake and Ruff 2007).

N. ferruginea has the same number of paired distal and sub distal papillae, however, the interramal cirri in this species begin on setiger three, rather than four in *N. caecoides* (Lovell 1997). *N. ferruginea* individuals have a distinct rust colored pigment in a V-shape pattern on prostomium in addition to transverse bars mid dorsally on the first 20 setigers and oblique stripes dorsolaterally (Hilbig 1997).

Ecological Information

Range: Type localities include Greenland and the Arctic (Hartman 1968). Known distribution is Alaska to northern California and circumboreal. Possibly introduced from the eastern United States (Blake and Ruff 2007).

Local Distribution: Coos Bay distribution includes many stations, especially those within South Slough. The distribution of *N. caeca* is much like that of the polychaete *Scoleteoma zonata*.

Habitat: Sand, mud or mixed sediments. Individuals also occur with eelgrass and prefer more mud than *Scoleteoma zonata* (Porch 1970).

Salinity: Collected at salinities of 30, but can tolerate lower salinities (i.e., freshwater of stream beds) (Porch 1970).

Temperature: A cold water species, *N. caeca* does not extend far southward to California.

Tidal Level: Intertidal (+ 0.15 m) to lower intertidal and depths of 1000 m (Rainer 1991).

Associates: Known associates include barnacles and the large polychaete, *Pista pacifica*.

Abundance: Not common, locally (Blake and Ruff 2007). In the St. Lawrence Estuary (Québec, Canada), most individuals were observed in the lowest sampling sites (specific sampling heights not indicated, Caron et al. 1995).

Life-History Information

Reproduction: *Nephtys caeca*, as is the case for other *Nephtys* species, are free-spawning with pelagic larval development that proceeds via a trochophore larva (Fernald et al. 1987; Crumrine 2001; Pleijel and Rouse 2006). In the St. Lawrence Estuary (Québec, Canada), oocyte maturation occurred in the late summer to autumn, oocyte diameters were approximately 140–160 μm (Caron et al. 1995) and ripe adults spawn into their temporary burrows (Bently et al. 1984). However, in the River Tyne Estuary (United Kingdom), individuals are known to spawn in late spring or early summer (Olive 1977).

Larva: Nephtyid trochophore larvae have a pair of eyes, dome-shaped prostomium and barrel-shaped body. They have well developed prototrochs and telotrochs, with neurotrochs present in young larvae. They are common in plankton samples and are recognized by their shape and species-specific bright body colors (Lacalli 1980; Fernald et al. 1987). Early trochophore larvae of *Nephtys caeca* have been described (Thorson 1946; Lacalli 1980). They have dull red to brown pigmentation on the episphere, prostomium and pygidium. The posterior pigmentation is arranged in two bands, one anterior to and the other posterior to the pygidium (Lacalli 1980). They also have an olive colored gut and no blue pigmentation, a common characteristic of other nephtyid larvae (e.g., <http://invert-embryo.blogspot.com/2012/12/confirmed-identity-of-wild-caught.html>). Eight-setiger stages measure approximately 670 μm in length and have simple capillary setae (Lacalli 1980). Nephtyid trochophore and metatrochophore larvae are predatory (Fernald et al. 1987; Crumrine 2001).

Juvenile: The prostomium transitions from rounded to angular in newly metamorphosed individuals (Fig. 5, Lacalli 1980). Juveniles may possess eyes on one of the first three setigers that are usually, although not always (e.g. *N. cornuta*), lost in adults (*Nephtys*,

Hilbig 1997). Advanced larval or juvenile stages were collected benthically from the River Tyne Estuary and described by Olive in 1977. Unique features included yellow-brown pigmented prostomium with rusty brown pigment granules dorsally, green intestine becoming deep blue posteriorly, spade-shaped pygidium and both smooth and striated setae. The four pairs of anterior antennae only developed in advanced stages (Olive 1977). No larval settlement was observed intertidally in the St. Lawrence Estuary, suggesting sublittoral larval recruitment. Instead, juveniles were seen intertidally in June–July (1986) (Caron et al. 1995).

Longevity: Seven or more year life-span (United Kingdom, Olive 1977).

Growth Rate: Sexual maturity is reached in two years (United Kingdom, Olive 1977).

Food: *Nephtys caeca* adults are carnivorous and predation by them is known to regulate other infaunal populations within a community. They are a primary predator of *Macoma balthica* (St. Lawrence Estuary) and are known to feed on smaller conspecifics (Ambrose 1984; Caron et al. 2004). Juvenile *N. caeca*, however, are herbivores (Caron et al. 2004).

Predators:

Behavior: Individuals are active, and are good swimmers and burrowers (MacGinitie 1935). Bioturbation from *N. caeca* has been shown to homogenize particles in the first few centimeters of sediment while burrowing or moving (Piot et al. 2008).

Bibliography

1. AMBROSE, W. G. 1984. Increased emigration of the amphipod *Rhepoxynius abronius* (Barnard) and the polychaete *Nephtys caeca* (Fabricius) in the presence of invertebrate predators. *Journal of Experimental Marine Biology and Ecology*. 80:67-75.
2. BENTLEY, M. G., P. J. W. OLIVE, P. R. GARWOOD, and N. H. WRIGHT. 1984. The spawning and spawning mechanism of *Nephtys caeca* (Fabricius, 1780) and *Nephtys hombergi* Savigny, 1818 (Annelida, Polychaeta). *Sarsia*. 69:63-68.

3. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
4. CARON, A., L. BOUCHER, G. DESROSIERS, and C. RETIERE. 1995. Population-dynamics of the polychaete *Nephtys caeca* in an intertidal estuarine environment (Quebec, Canada). *Journal of the Marine Biological Association of the United Kingdom*. 75:871-884.
5. CARON, A., G. DESROSIERS, P. J. W. OLIVE, C. RETIERE, and C. NOZAIS. 2004. Comparison of diet and feeding activity of two polychaetes, *Nephtys caeca* (Fabricius) and *Nereis virens* (Sars), in an estuarine intertidal environment in Quebec, Canada. *Journal of Experimental Marine Biology and Ecology*. 304:225-242.
6. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
7. DNESTROVSKAYA, N. Y., and I. A. JIRKOV. 2011. Microscopical studies of *Nephtyid chaetae* (Annelida: Polychaeta: Nephtyidae) from Northern Europe and Arctic. *Italian Journal of Zoology*. 78:219-228.
8. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
9. HARTMAN, O. 1938. Review of the annelid worms of the family nephtyidae from the northeast pacific, with descriptions of five new species. *Proceedings of the United States National Museum*. 85:143-158.
10. HARTMAN, O. 1968. Atlas of the errantiate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
11. HILBIG, B. 1997. Family Nereididae, p. 291-316. *In*: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 4. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
12. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to Northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
13. LACALLI, T. C. 1980. A guide to the marine flora and fauna of the Bay of Fundy: polychaete larvae from Passamaquoddy Bay. Canadian Technical Report of Fisheries and Aquatic Sciences. 940:1-27.
14. LOVELL, L. L. 1997. A review of six species of *Nephtys* (Cuvier, 1817) (Nephtyidae: Polychaeta) described from the eastern Pacific. *Bulletin of Marine Science*. 60:350-363.
15. MACGINITIE, G. E. 1935. Ecological aspects of a California marine estuary. *American Midland Naturlist*. 16:629-765.
16. OLIVE, P. J. W. 1977. Life-history and population-structure of polychaetes *Nephtys caeca* and *Nephtys hombergii* with special reference to growth rings in teeth. *Journal of the Marine Biological Association of the United Kingdom*. 57:133-150.
17. PIOT, A., A. ROCHON, G. STORA, and G. DESROSIERS. 2008. Experimental study on the influence of bioturbation performed by *Nephtys caeca* (Fabricius) and *Nereis virens* (Sars) annelidae on the distribution of dinoflagellate cysts in the sediment. *Journal of Experimental Marine Biology and Ecology*. 359:92-101.
18. PLEIJEL, F., and G. W. ROUSE. 2006. Phyllodocida, p. 431-496. *In*: Reproductive biology and phylogeny of annelida. G. W. Rouse and F. Pleijel (eds.). Science Publications, Enfield, NH.

19. PORCH, L. L. 1970. Polychaetes of Coos Bay. *In*: OIMB Unpublished Student Report, Summer 1970.
20. RAINER, S. F. 1991. The genus *Nephtys* (Polychaeta, Phyllodocida) of Northern Europe: a review of species, including the description of *N. pulchra* sp-n and a key to the Nephtyidae. *Helgolander Meeresuntersuchungen*. 45:65-96.
21. THORSON, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Oresund). *Medd fra Komm Danmarks Fisk Havundersogelser Ser Plankton*. 4:1-523.

Updated 2015

Nephtys caecoides

A sand worm

Phylum: Annelida
Class: Polychaeta
Order: Phyllodocida
Family: Nephtyidae

Description

Size: Individuals up to 100 mm in length and 5–8 mm in width, with up to 129 segments (Hartman 1968; Hilbig 1997). The illustrated specimen has 115 segments (Fig. 1).

Color: A strong pigment pattern on prostomium and first few segments (Fig. 2) persists through preservation. Body usually steel to dark grey (Hartman 1938).

General Morphology: Anterior cylindrical in cross-section and becomes slender and rectangular posteriorly (Nephtyidae, Blake and Ruff 2007).

Body: Trim, stiff and slender in appearance (Hartman 1938), rectangular in cross section (Hartman and Reish 1950). Anterior third is stout and wide, while the middle and posterior regions become slender and more flexible (Hilbig 1997). First segment is incomplete dorsally (Hartman 1968) (Fig. 2).

Anterior: Prostomium is trapezoidal or rounded and changes shape when proboscis is everted (Fig. 2) (Hilbig 1997).

Trunk: Thick with widely separated parapodial rami (Fig. 1, 5).

Posterior: Pygidium bears long caudal cirrus that is sometimes lost during collection or preservation.

Parapodia: Parapodia are biramous and rami are widely separated, densely packed and their setae are fan-shaped (Nephtyidae, Blake and Ruff 2007). Both noto- and neuropodia are rounded in the worm posterior (Fig. 5b) and the acicular lobes are incised in the middle of the worm (Fig. 5a). First parapodial pair pointed anterior (Hilbig 1997). Another defining characteristic of the Nephtyidae are the interramal cirri that are inserted just beneath dorsal cirri, which are small, in anterior setigers (Blake and Ruff 2007) (Fig. 5). Beginning with the fourth setiger, and continuing to within 10–20 setigers from worm posterior, there is a recurved cirrus between the parapodial lobes (Fig. 5) (Lovell 1997). In juvenile specimens, this can be nearly straight (Fauchald 1977).

The interramal cirrus is larger than the dorsal cirrus, except in the last nine segments (Hartman 1968).

Setae (chaetae): All nephtyid setae are simple and the setae of both rami are of similar morphology. Overall, there are four main types of nephtyid setae including capillary (e.g. spinose), barred (which are pre-acicular), lyrate and setae with spines (Dnestrovskaya and Jirkov 2011). *Nephtys caecoides* exhibits three setal types; 1) a bunch of short, stiff and slender barred setae (pre-acicular) (Fig. 4a, b); 2) post-acicular setae with upper fascicle of spinulose capillaries and large middle fascicle with wide spinose setae (Fig. 4c); 3) neurosetae with upper smooth capillaries and spinose setae in middle fascicle and spinulose capillaries in lower fascicle. Setae of first parapodium are pointed anteriorly and the remainder are lateral (Fig. 2) (Hilbig 1997). A single acicula is present in each ramus, and is transparent or yellow and tapers to a fine tip (Hilbig 1997).

Eyes/Eyespots: Absent in adults (Hilbig 1997).

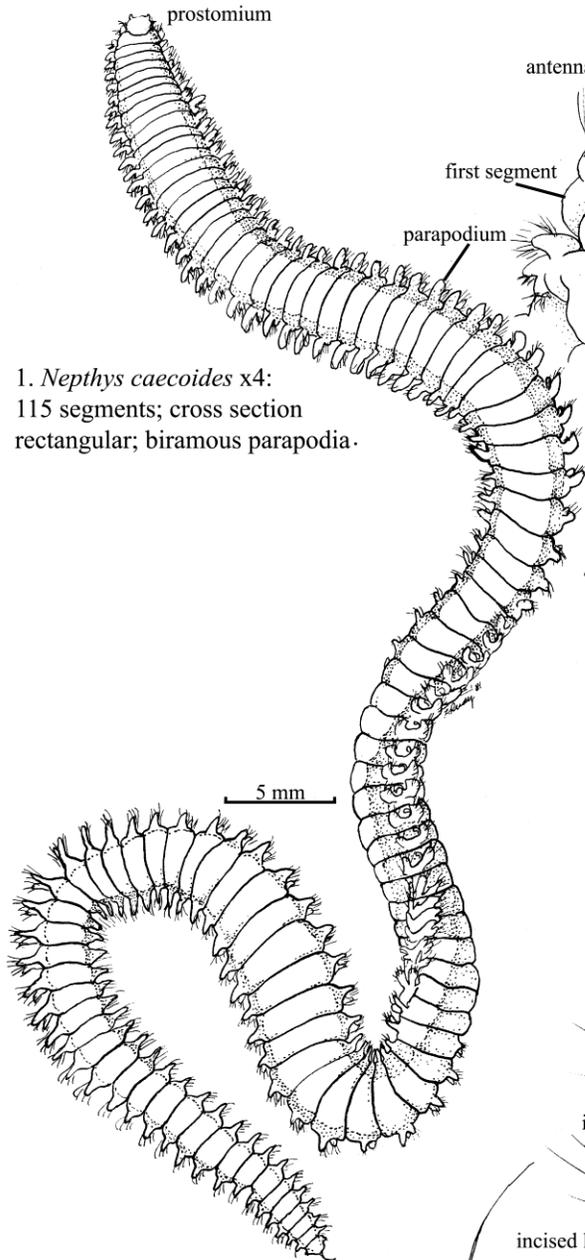
Anterior Appendages: Prostomium bears four small simple antennae, in two pairs which are widely separated. One pair of nuchal organs present (Hilbig 1997).

Branchiae: The interramal cirri, which are inserted just beneath each dorsal cirrus, are sometimes called branchiae (Blake and Ruff 2007).

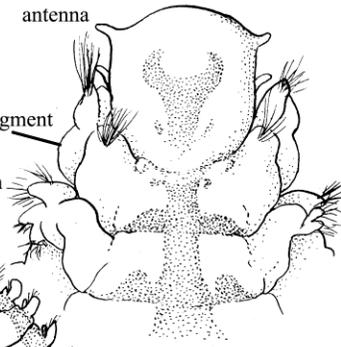
Burrow/Tube:

Pharynx: Bears short and wide proboscis with a variety of papillae, their number and arrangement is of taxonomic significance (Blake and Ruff 2007). The proboscis in *Nephtys* species can be divided into three distinct regions including the proximal, sub-distal and distal (Lovell 1997) (Fig. 3). In *N. caecoides* there are 20 pairs of distal papillae, an unpaired mid-dorsal papilla and 22 rows of sub-terminal papillae with 3–6 papillae per row (five per row in the illustrated specimen). Mid-dorsal and mid-ventral distal areas of the

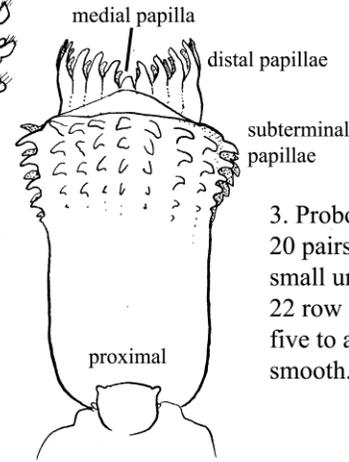
Nephtys caecoides



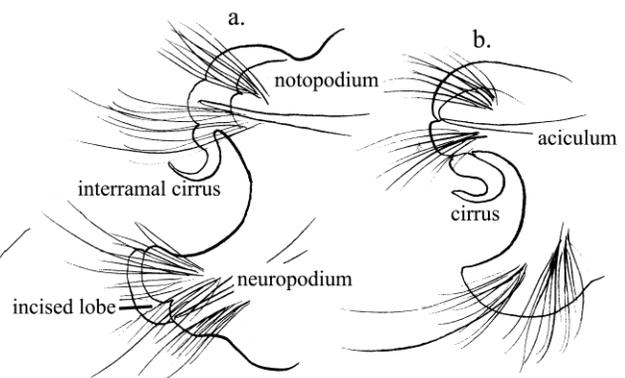
1. *Nephtys caecoides* x4:
115 segments; cross section
rectangular; biramous parapodia.



2. Prostomium (dorsal view):
flattened, pentagonal; eyeless;
four small antennae, first
segment incomplete dorsally;
strong pigment pattern.

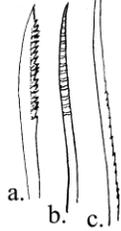


3. Proboscis, everted x12:
20 pairs distal papillae, a
small unpaired medial papilla;
22 row subterminal papillae,
five to a row; proximal surface
smooth.



5. Parapodia, (a.) medial and (b.) posterior x30:
biramous, well separated; long, recurved interramal
cirri beginning on setiger five; noto- and neurosetae in
fan-shaped fascicles (bunches); acicular lobes incised.

4. Parapodial setae:
a. short, barbed
b. pre-acicular setae;
transversely barred.
c. post-acicular seta; single
lateral barbs .



proboscis are without papillae and smooth (Lovell 1997; Hilbig 1997) (Fig. 3).

Genitalia:

Nephridia:

Possible Misidentifications

Worms of the family Nephtyidae can be distinguished by their anteriorly cylindrical and posteriorly rectangular bodies (in cross section), well-developed bi-lobed parapodia, interramal cirri, four small prostomial antennae, and eversible globular proboscis with terminal rows of papillae. They are strong and muscular worms that can be good burrowers and strong swimmers (Blake and Ruff 2007). Nephtyids superficially resemble the genus *Nereis*, however, they have no long anterior appendages (tentacular cirri) and their proboscis armature is quite different (Kozloff 1993). The distinctive taxonomic characters of *N. caecoides* include 20 distal paired papillae, 22 rows of sub-distal papillae with 3–6 papillae per row, an unpaired mid-dorsal papilla and interramal cirri beginning on setiger four (Lovell 1997).

Some *Nephtys* species are distinguished from each other by very fine morphological details. The species most closely related to and difficult to differentiate from *N. caecoides* include *N. caeca* and *N. californiensis*. *N. caeca* is slightly larger, iridescent, with no prostomial pigmentation and a rough proboscis with no unpaired medial papilla. Furthermore, this species has interramal cirri beginning on the fifth or sixth setiger, not the fourth (as in *N. caecoides*). This is a northern species, which is locally rare, and likely introduced from the eastern United States (Blake and Ruff 2007). *N. californiensis* is found mostly on the outer coast, or if in bays, only in very clean coarse sand. It has a distinctive V-shaped pigment pattern (sometimes with red spot at center) of pigmentation on the lower end of the prostomium, a smooth proboscis without medial papilla, soft silky flowing setae and interramal cirri beginning on the third setiger.

Three other *Nephtys* species that are not so easily confused with *N. caecoides*. *N. cornuta*, a small species (less than 15 mm in length) that can be identified by its distinctive bifid ventral and

posterior antennae. This species often retains larval eyes on the third setiger, a feature which is usually lost in other closely related species (Blake and Ruff 2007). *N. cornuta* can also be differentiated because it has 18 distal paired papillae (instead of 20 in *N. caecoides*) and interramal cirri that begin on setiger five (rather than four in *N. caecoides*) (Lovell 1997). *N. punctata* is much like *N. caeca* in size and form (Hartman 1938), but has interramal cirri beginning on setiger 8–10, and with incised acicular lobes in the anterior parapodia. This species is large and muscular with wide body and short parapodia and is currently only reported in southern California (Hilbig 1997; Blake and Ruff 2007)

N. parva, colorless except for a dark spot in the middle of its prostomium (Hartman 1968), a smooth proboscis proximally, no medial papilla, eyespots on its third setiger and interramal cirri beginning on the fourth setiger. The type material from this species is suspected to have been miscurated and the holotype appears to be that of *N. cornuta*, while the species description and paratypes match *N. caecoides* more closely. Thus, this species is not a currently a valid taxon (Lovell 1997; Blake and Ruff 2007).

N. ferruginea has the same number of paired distal and sub-distal papillae, however, the interramal cirri in this species begin on setiger three, rather than four in *N. caecoides* (Lovell 1997). *N. ferruginea* individuals have a distinct rust colored pigment in a V-shape pattern on prostomium in addition to transverse bars mid dorsally on the first 20 setigers and oblique stripes dorsolaterally (Hilbig 1997).

Ecological Information

Range: Type locality is Tomales Bay, California (Hartman 1968). Known range includes western Canada to southern California.

Local Distribution: Coos Bay distribution includes many stations, especially those within the South Slough. The distribution of *N. caecoides* is very close to *Scoletoma zonata* but occurs in sandier mud (Porch 1970).

Habitat: Mud, sand and mixed sediments of bays and lagoons. *N. caecoides* also occurs in eelgrass flats (Hartman 1938) but is not found in areas with large amounts of silt (Clark and Haderlie 1962). Instead this species prefers fine, stable substrate.

Salinity: Can tolerate low salinities, (i.e. freshwater stream beds) (Porch 1970).

Temperature:

Tidal Level: Intertidal to littoral depths (one specimen from 46–106 meters) (Hartman and Reish 1950). Densest populations at Bodega Bay at + 0.32 meters and at -0.52 meters MLLW (Clark and Haderlie 1962). Individuals observed from 0.0 m to +1.2 m, with 15 specimens collected at 0.0 m, 7 specimens at +0.9 m and 1 specimen at +1.2 m (Johnson 1970).

Associates: *Nephtys caeca* has much the same habitat (Porch 1970).

Abundance: One of the most common nephtyids in California where San Francisco Bay densities were recorded at 130 individuals/m² (Jones 1961) and Bodega Bay densities were 32 individuals/m² (Clark and Haderlie 1962). The most commonly found nephtyid in Coos Bay and distribution is a function of protection from exposure, rather than other physical factors (e.g. salinity or temperature, Porch 1970).

Life-History Information

Reproduction: The reproduction and larval development of *N. caecoides* is not known. However, *Nephtys* species are usually free-spawning with pelagic development that proceeds via a trochophore larva (e.g. *N. caeca*, Fernald et al. 1987; Crumrine 2001).

Larva: Nephtyid trochophore larvae have a pair of eyes, dome-shaped prostomium and barrel-shaped body. They have well developed prototrochs and telotrochs, with neurotrochs present in young larvae. Nephtyid larvae are common in plankton samples and are recognized by their shape and species-specific bright body colors (Lacalli 1980; Fernald et al. 1987). A locally collected larva identified to the genus *Nephtys* with DNA sequence data had distinct red pigment bands near the prototroch and telotroch and blue pigment within the gut (<http://invert-embryo.blogspot.com/2012/12/confirmed-identity-of-wild-caught.html>). Nephtyid

trochophore and metatrochophore larvae are predatory (Fernald et al. 1987; Crumrine 2001).

Juvenile: The prostomium becomes angular rather than rounded in newly metamorphosed individuals (Fig. 5, Lacalli 1980). Juveniles may possess eyes on one of the first three setigers that are usually, although not always (e.g. *N. cornuta*), lost in adults (Hilbig 1997).

Longevity:

Growth Rate:

Food: *Nephtys caecoides* is carnivorous (Clark and Haderlie 1962).

Predators:

Behavior: Individuals are very active, and are good swimmers and burrowers.

Bibliography

1. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. T. Carlton (ed.). University of California Press, Berkeley, CA.
2. CLARK, R. B., and E. C. HADERLIE. 1962. The distribution of *Nephtys californiensis* and *N. caecoides* on the California coast. *Journal of Animal Ecology.* 31:339-357.
3. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In: Identification guide to larval marine invertebrates of the Pacific Northwest.* A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
4. DNESTROVSKAYA, N. Y., and I. A. JIRKOV. 2011. Microscopical studies of *Nephtyid chaetae* (Annelida: Polychaeta: Nephtyidae) from Northern Europe and Arctic. *Italian Journal of Zoology.* 78:219-228.
5. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County Science Series.* 28:1-190.
6. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In: Reproduction and development of marine invertebrates of the northern Pacific coast.* M. F.

- Strathmann (ed.). University of Washington Press, Seattle, WA.
7. HARTMAN, O. 1938. Review of the annelid worms of the family Nephtyidae from the northeast pacific, with descriptions of five new species. Proceedings of the United States National Museum. 85:143-158.
 8. —. 1968. Atlas of the errantiate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
 9. HARTMAN, O., and D. J. REISH. 1950. The Marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
 10. HILBIG, B. 1997. Family Nereididae, p. 291-316. *In*: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 4. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
 11. JOHNSON, R. G. 1970. Variations in diversity within benthic marine communities. *American Naturalist*. 104:285-300.
 12. JONES, M. L. 1961. A quantitative evaluation of the benthic fauna off Point Richmond, California. University of California Publications in Zoology. 67:219-320.
 13. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
 14. LACALLI, T. C. 1980. A guide to the marine flora and fauna of the Bay of Fundy: polychaete larvae from Passamaquoddy Bay. Canadian Technical Report of Fisheries and Aquatic Sciences. 940:1-27.
 15. LOVELL, L. L. 1997. A review of six species of *Nephtys* (Cuvier, 1817) (Nephtyidae: Polychaeta) described from the eastern Pacific. *Bulletin of Marine Science*. 60:350-363.
 16. PORCH, L. L. 1970. Polychaetes of Coos Bay. *In*: OIMB Unpublished Student Report, Summer 1970.

Updated 2015

Neanthes brandti

A clam bed worm

Phylum: Annelida
Class: Polychaeta
Order: Phyllodocida
Family: Nereididae

Taxonomy: *Neanthes brandti* has been placed in the genera *Nereis* and, most recently, *Alitta*. Depending on the author, *Neanthes* is currently considered a separate or subspecies to the genus *Nereis* (Hilbig 1997). The genus *Alitta* was originally designated for the species, *A. virens*, based on parapodial morphology. Later, *A. brandti* was added to this genus. Although, most authors regard *Neanthes* and *Alitta* as synonyms, there is evidence to suggest that *Alitta* is a monophyletic and a separate taxon to *Neanthes* (Bakken and Wilson 2005). Currently, *Neanthes brandti* is the name seen in local intertidal guides (e.g., Blake and Ruff 2007), but this name could change to *Alitta brandti* in the near future. Furthermore, *N. brandti* is one of three species in a closely related cryptic species complex which has been suggested to be not three, but the single, widely distributed species – *N. virens* (Breton et al. 2004).

Description

Size: Atokous or sexually immature individuals up to 185 mm in length, having 166 segments. Epitokous (heteronereids) are 300- 600 mm in length, 18 mm in width, having 230 segments (Hartman 1968; Fernald et al. 1987).

Color: Usually a dark iridescent green-brownish or blueish, with a ventrum more pale than dorsum (Hartman 1968).

General Morphology: Thick worms that are rather wide for their length (Fig. 1).

Body: Individuals are flattened dorso-ventrally and extremely active. Nereids are recognizable by their anterior appendages including two prostomial palps and four peristomial tentacular cirri (see **Anterior appendages**) (Blake and Ruff 2007).

Anterior: Prostomium short, broad and not as long as peristomium (Fig. 2). The peristomium is apodous and asetigerous.

Trunk: Thick segments that are wider than they are long, gently tapers to posterior (Fig. 1).

Posterior: Pygidium bears two slender ventrolateral anal cirri (Fig. 1) (Blake and Ruff 2007).

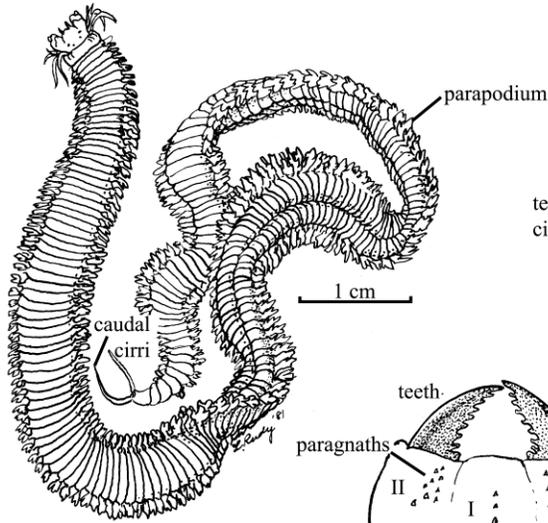
Parapodia: The first two setigers are uniramous. All other parapodia are biramous (Nereididae, Blake and Ruff 2007) where both notopodia and neuropodia have acicular lobes and each lobe bears 1–3 additional lobes (above and below) called ligules (Blake and Ruff 2007). The posterior notopodial lobes broadly expanded and leaf-like. All other lobes are small (Fig. 6). Dorsal cirri are short and inserted halfway along dorsal (notopodial) lobe, while ventral cirri are inserted at the base of the neuropodial lobe (Fig. 6). The parapodia of epitokous individuals are modified for swimming and are wide and plate-like (Hilbig 1997).

Setae (chaetae): Setae are compound and can be blunt (falcigerous) or hair-like (spinigerous) (Nereididae, Blake and Ruff 2007). Compound setae can be described as heterogomph, meaning that the two basal prongs are of unequal length, or homogomph, where basal prongs are of equal length (Fig. 5). Notosetae are composite spinigers only (Fig. 5) (*Neanthes*, Pettibone 1963; Fauchald 1977; Hilbig 1997). Neurosetae are both composite spinigers and short shafted falcigers (Fig. 5).

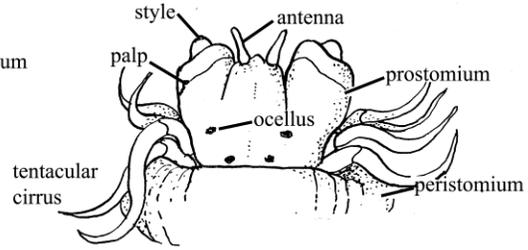
Eyes/Eyespots: Two pairs of eyes in trapezoidal arrangement on prostomium (Fig. 2) (Nereididae, Hartman 1968; Blake and Ruff 2007). The eyes of epitokous individuals are enlarged (Hilbig 1997).

Anterior Appendages: Palps at sides of prostomium are thick at bases and each have a small style (Fig. 2). The palps of epitokous individuals are larger than sexually immature individuals (Hilbig 1997). The prostomium also bears two short and conical antennae (Fig. 2). Four pairs of smooth tentacular cirri are found on the peristomium and second dorsal pair is the longest.

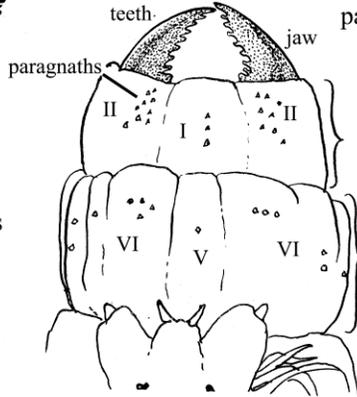
Neanthes brandti



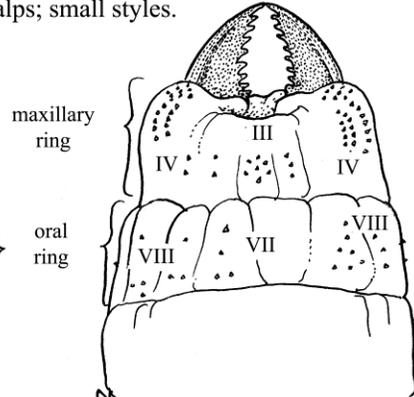
1. *Neanthes brandti* x2:
dark green color; biramous
parapodia; caudal cirri.



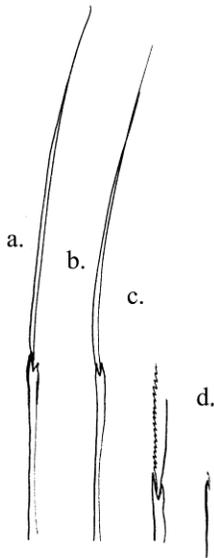
2. Prostomium (dorsal view) x12:
four small ocelli; antennae-one small
pair; tentacular cirri-four pairs; large
palps; small styles.



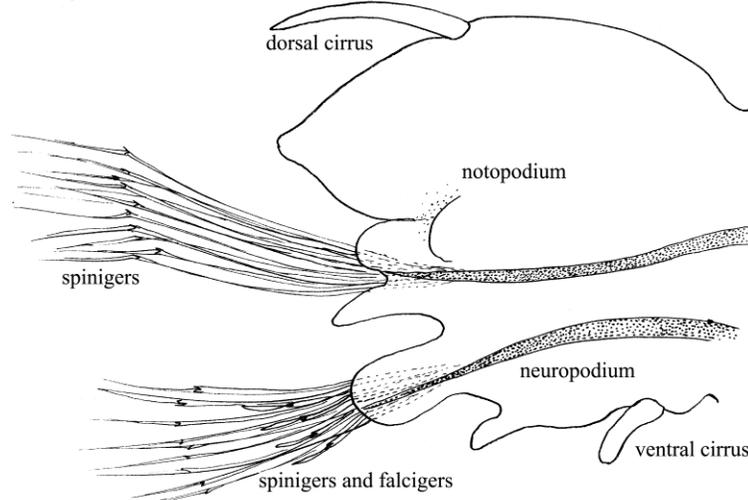
3. Everted proboscis (dorsal
view) x12 conical paragnaths on
oral and maxillary rings; jaws 6-8
teeth; paragnaths area I:3 in tandem,
II:7-8+ in patch, V:0-1, VI:median
band, 4-5 rows.



4. Everted proboscis (ventral
view) x12: paragnaths area
III: dense patch, IV: several rows
(patch), VII: broad band 4-5 rows,
VIII: broad band, 4-5 rows.



5. Setae x300:
a. heterogomph spiniger
b. homogomph spiniger
c. heterogomph falciger
d. homogomph falciger



6a. Posterior parapodium: biramous, dorsal notopodium
and ventral neuropodial lobes ; notopodial lobe leaf-like;
dorsal cirrus medial.

Branchiae: Absent (Blake and Ruff 2007).

Burrow/Tube: Nereids secrete and live in mucous-lined tubes (Hilbig 1997).

Pharynx: The pharynx bears a distinct eversible proboscis. The everted proboscis has two rings, oral (or proximal) and distal (or maxillary) and terminates with two fang-shaped jaws (Figs. 3, 4). The oral ring is used largely in burrowing, while the distal ring is used in feeding (Barnes and Head 1977). Each ring is equipped with many papillae and conical paragnaths and their patterns are taxonomically relevant. Area I is composed of three cones in tandem; Area II, III, IV are each with many cones in dense patches; Area V has zero to one cone (Banse and Hobson 1974); Area VI has a median row of four to five large cones; Areas VII and VIII are each with a broad band of many cones (Hartman 1968) (*N. brandti* has at least four to five rows) (Figs. 3, 4) (Banse and Hobson 1974).

Genitalia:

Nephridia:

Possible Misidentifications

The prostomia of nereid worms are quite alike, with four eyes, a pair of frontal antennae and biarticulate palps, and 3–4 pairs of tentacular cirri. The genus *Neanthes* currently, includes 3–4 local species (Blake and Ruff 2007). *Neanthes* species have only homogomph spinigerous setae in the posterior notopodia, a trait it shares with *Hediste* but without the fused falcigers. The genus *Neanthes* is further distinguished by having only conical paragnaths on both proboscis rings, and biramous parapodia with composite setae (Hartman and Reish 1950).

Neanthes brandti has been at times considered a subspecies or a synonym of *N. virens*, the large, coldwater form (Breton et al. 2004). This latter species, however, has only a few paragnaths on its proboscis rings, (i.e. 2–3 rows in Areas VII, VIII), not many as in *N. brandti* (4–5 rows in Areas VII, VIII). The prostomium of *N. virens* is small and triangular, its eyes are small and on the posterior half of the prostomium. It has short antennae, and massive palps. These species exhibit overlapping geographic distributions and it is possible that they are the same species (Breton et al. 2004).

Neanthes succinea is one of the most common nereids in the NE Pacific, but is recognizable from *N. brandti* by its very enlarged posterior notopodial lobes, with a small distal dorsal cirrus attached at the end of the lobe (Blake and Ruff 2007). Furthermore, it has a heteronereid form and *N. limnicola* does not. *N. succinea* is thought to be a more southern form (although it has been reported from Netarts Bay).

Neanthes limnicola is usually pale and translucent, not dark green and its posterior parapodial lobes are not expanded like those of *N. brandti*.

Neanthes have spinigerous notosetae only (Hilbig 1997). The morphologically similar genus, *Nereis sensu stricto*, is characterized by species with spinigerous notosetae in the anterior half of the body and falcigerous notosetae posteriorly (Pettibone 1963; Smith 1959). Common *Nereis* species include the very abundant *Nereis vexillosa*, an olive green to brown worm found in many diverse marine environments, especially in mussel beds. It has greatly elongated, strap-like notopodial lobes in the posterior parapodia. *Nereis eakini*, from rocky habitats, has a long prostomium and proboscis rings covered with small round paragnaths. The bright green *Nereis grubei* has greatly expanded posterior notopodial parapodial lobes and no paragnaths in Area V of the proboscis. *Nereis procera* is subtidal in sand, has tiny eyes, a very long body, and unusually inconspicuous paragnaths on its proboscis (Hartman 1968). The genus *Nereis* differs from *Hediste* because members of the latter genus has 1–3 fused falcigers on the supra-acicular bunch of posterior neuropodial setae (no local species are known, Blake and Ruff 2007).

Ecological Information

Range: Type locality is coastal Siberia. Known range includes northeast Pacific to southern California (Hartman 1968).

Local Distribution: Coos Bay distribution includes sites along the South Slough in Charleston (Hartman and Reish 1950).

Habitat: Known habitats are highly variable with individuals found in sand bars, thick mud (Kozloff 1974), and *Enteromorpha* beds (MacGinitie and MacGinitie 1949). Largest

specimens occur in fine mud and eelgrass beds rather than in pure sand. *N. brandti* is very rare in sulfite-polluted areas (Porch 1970).

Salinity:

Temperature:

Tidal Level: Low intertidal (Hartman 1968) where individuals burrow deeply in sand.

Associates:

Abundance: A common nereid in Coos Bay and also abundant in eelgrass beds (Pettibone 1963).

Life-History Information

Reproduction: Epitokous stages begin swarming and are attracted to night-lights in June–August (Washington, Fernald et al. 1987). These epitokes provide observers with one of the most spectacular displays of nereid swarming (Porch 1970). The sexually mature (epitokous) animals swim wildly at night on the water's surface, their medial parapodial lobes swollen for swimming. After expelling sperm and eggs, the distended worms will die.

Larva: The larval development of *N. brandti* is not known, and development varies in the Nereididae. Some species have embryos that are fertilized and develop in the plankton, while others develop in benthic egg masses. Their trochophore larval stage is usually reduced and most nereids hatch as nectochaetes (Fernald et al. 1987; Crumrine 2001). Many larvae are lecithotrophic until their pharynx is fully developed. Finally, nereid larvae tend not to acquire many segments in the plankton, and instead do so once they have settled into the benthos (Fernald et al. 1987).

Juvenile:

Longevity:

Growth Rate:

Food: Fecal castings, which are similar to the lug worm (see *Abarenicola pacifica*), are small and contain seaweed. Although some nereids are carnivorous (Blake and Ruff 2007), many are herbivorous and use their jaws to tear apart and eat pieces of algae (Fernald et al. 1987; Kozloff 1993). Immature worms appear to eat *Ulva*, *Enteromorpha* (MacGinitie and MacGinitie 1949).

Predators:

Behavior: *Neanthes brandti* are fast swimmers with swimming speed between 50–80 mm/sec (Haderlie 1980).

Bibliography

1. BAKKEN, T., and R. S. WILSON. 2005. Phylogeny of nereidids (Polychaeta, Nereididae) with paragnaths. *Zoologica Scripta*. 34:507-547.
2. BANSE, K., and K. D. HOBSON. 1974. Benthic errantiate polychaetes of British Columbia and Washington. Fisheries and Marine Service, Ottawa, Canada.
3. BARNES, R. S. K., and S. M. HEAD. 1977. Variation in paragnath number in some British populations of estuarine polychaete *Nereis diversicolor*. *Estuarine and Coastal Marine Science*. 5:771-781.
4. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
5. BRETON, S., F. DUFRESNE, G. DESROSIERS, and P. BLIER. 2004. Morphological variation in *Nereis (Neanthes) virens* (Polychaeta : Nereididae) populations. *Journal of the Marine Biological Association of the United Kingdom*. 84:983-985.
6. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
7. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County Science Series*. 28:1-190.
8. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F.

- Strathmann (ed.). University of Washington Press, Seattle, WA.
9. HADERLIE, E. C. 1980. Polychaeta: the marine annelid worms, p. 448-489. *In: Intertidal invertebrates of California.* R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
 10. HARTMAN, O. 1968. Atlas of the errantiate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
 11. HARTMAN, O., and D. J. REISH. 1950. The Marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
 12. HILBIG, B. 1997. Family Nereididae, p. 291-316. *In: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel.* Vol. 4. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
 13. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
 14. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
 15. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 16. PETTIBONE, M. 1963. Aphroditidae through Trochochaetidae. *In: Marine polychaete worms of the New England Region.* Vol. 1. Smithsonian Institution, Washington, D.C.
 17. PORCH, L. L. 1970. Polychaetes of Coos Bay. *In: OIMB Unpublished Student Report, Summer 1970.*
 18. SMITH, R. I. 1959. The synonymy of the viviparous polychaete *Neanthes lighti* Hartman (1938) with *Nereis limnicola* Johnson (1903). *Pacific Science.* 13:349-350.

Updated 2015

Neanthes limnicola

A mussel worm

Phylum: Annelida
Class: Polychaeta
Order: Phyllodocida
Family: Nereididae

Taxonomy: Depending on the author, *Neanthes* is currently considered a separate or subspecies to the genus *Nereis* (Hilbig 1997). *Nereis sensu stricto* differs from the genus *Neanthes* because the latter genus includes species with spinigerous notosetae only. Furthermore, *N. limnicola* has most recently been included in the genus (or subgenus) *Hediste* due to the neuropodial setal morphology (Sato 1999; Bakken and Wilson 2005; Tusuji and Sato 2012). However, reproduction is markedly different in *N. limnicola* than other *Hediste* species (Sato 1999). Thus, synonyms of *Neanthes limnicola* include *Nereis limnicola* (which was synonymized with *Neanthes lighti* in 1959 (Smith)), *Nereis (Neanthes) limnicola*, *Nereis (Hediste) limnicola* and *Hediste limnicola*. The predominating name in current local intertidal guides (e.g. Blake and Ruff 2007) is *Neanthes limnicola*.

Description

Size: Individuals 25–45 mm in length, 2.5–4 mm in width (without parapodia) and have 45–82 segments (Hartman 1938). The illustrated specimen, from Coos Bay, was 25 mm long.

Color: The illustrated specimen was pale, translucent to pale yellow green.

General Morphology: Very thick worms that are rather wide for their length (Fig. 1).

Body: Individuals are flattened dorso-ventrally and extremely active. Nereids are recognizable by their anterior appendages including two prostomial palps and four peristomial tentacular cirri (see **Anterior appendages**) (Blake and Ruff 2007).

Anterior: Prostomium trapezoidal, wider than long, with a longitudinal depression (Fig. 2b).

Trunk: Very thick segments that are wider than they are long, gently tapers to posterior (Fig. 1).

Posterior: Pygidium bears two, styliform ventrolateral anal cirri that

are as long as last seven segments (Fig. 1) (Hartman 1938).

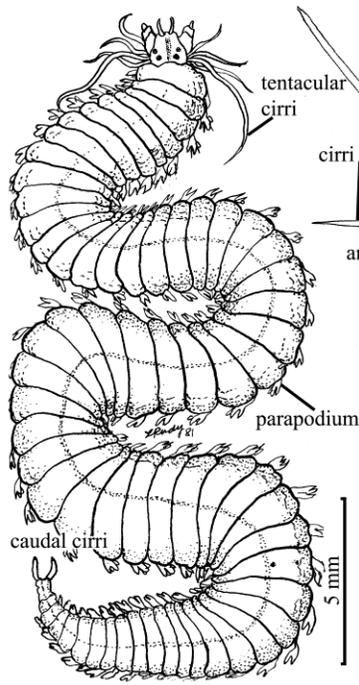
Parapodia: The first two setigers are uniramous. All other parapodia are biramous (Nereididae, Blake and Ruff 2007) where both notopodia and neuropodia have acicular lobes and each lobe bears 1–3 additional, medial and triangular lobes (above and below), called ligules (Blake and Ruff 2007) (Figs. 1, 5). The notopodial ligule is always smaller than the neuropodial one. The parapodial lobes are conical and not leaf-like or globular as in the family Phyllodocidae. (A parapodium should be removed and viewed at 100x for accurate identification). Notopodial lobes at posterior end of animal are normal, not elongate, but smaller than anterior lobes (Hartman 1938).

Setae (chaetae): All setae are composite. The notopodia (Fig. 5) bears only one kind of seta – homogomph spinigers, which are long, sharp composite spines with basal prongs of equal length (Fig. 4a). The neuropodia (Fig. 5) contain several each of three kinds of setae – homogomph and heterogomph spinigers, and heterogomph falcigers (with basal prongs of unequal length) (Fig. 4a, b, c). They also have heterogomph and homogomph falcigers with blunt, short and curved setae (Fig. 4c) (Fauchald 1977). *N. limnicola* has one special fused falciger in the upper acicular neuropodium (Figs. 4d, 5) (Johnson 1903). (Differentiation among these setae must be made with a compound microscope after placing the parapodium in glycerin or mounting medium, on a slide.) Acicula or heavy, black spines, are present at the base of each parapodial lobe (Fig. 5).

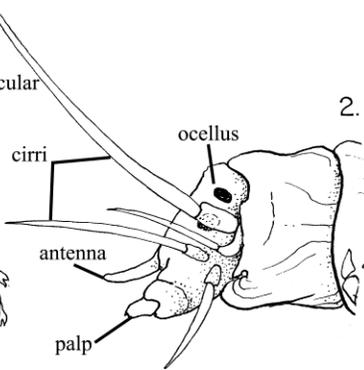
Eyes/Eyespots: Two pairs of eyes in trapezoidal arrangement on prostomium (Fig. 2b) (Nereididae, Hartman 1968; Blake and Ruff 2007). The eyes of epitokous individuals are enlarged (Hilbig 1997).

Anterior Appendages: One small pair of frontal antennae, which are separated at their bases, occurs on the prostomium (Fig. 2b). Also on the prostomium are a pair of palps,

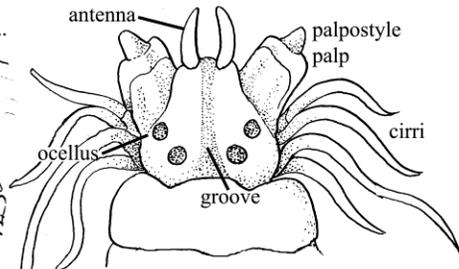
Neanthes limnicola



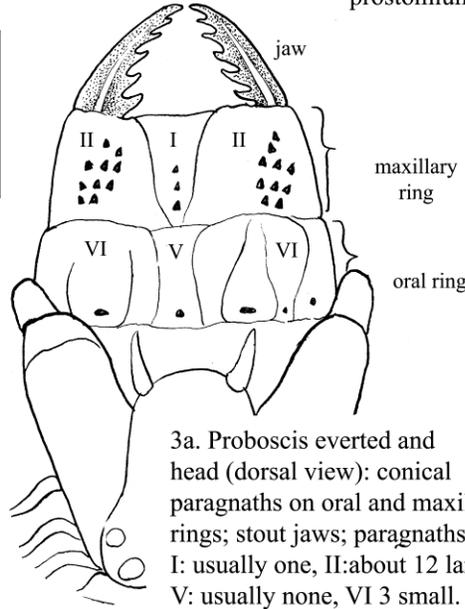
1. *Neanthes limnicola* x8.5: typical nereid tentacular cirri; body 25-45 mm long, 45-82 segments; pale, translucent; two caudal cirri.



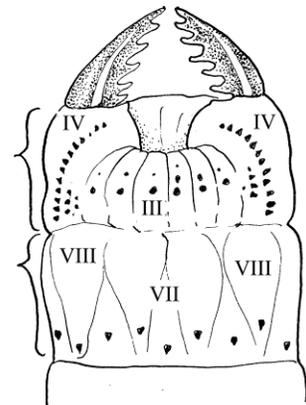
2a. Prostomium (lateral view) x30.



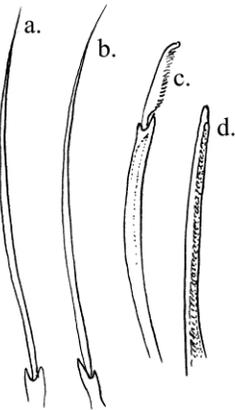
2b. Prostomium (dorsal view) x30: four pairs tentacular cirri; one small pair antennae; one pair palpi with palpostyles; four ocelli; prostomium trapezoidal, grooved.



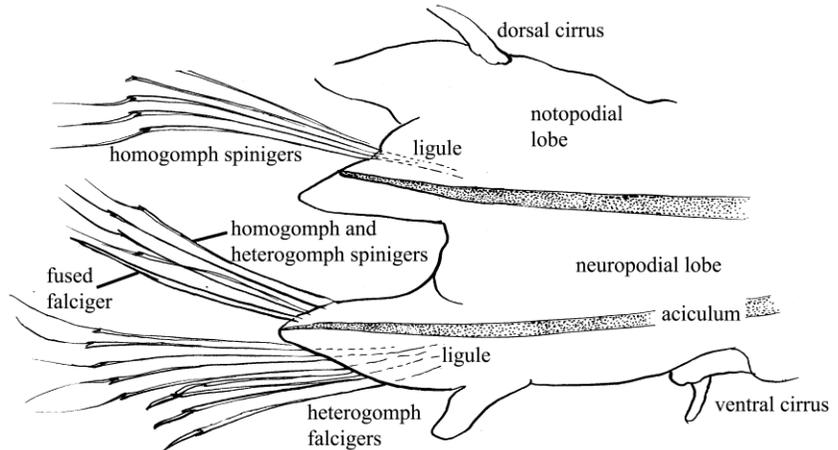
3a. Proboscis everted and head (dorsal view): conical paragnaths on oral and maxillary rings; stout jaws; paragnaths area I: usually one, II: about 12 large, V: usually none, VI 3 small.



3b. Proboscis everted (ventral view): paragnaths area III: 20-25, IV: crescent, 30-35, VII: continuous rows, VIII: continuous rows.



4. Setae:
a. homogomph spiniger
b. heterogomph spiniger
c. heterogomph falciger
d. fused falciger



5a. 60th parapodium x100: biramous, notopodium dorsal and neuropodium ventral; all lobes conical; small dorsal ligule.

with cylindrical processes and small hemispherical palpostyles at the distal ends (Fig. 2b). Four pairs of tentacular cirri are found on the peristomium. The second of dorsal pairs longest (Fig. 2b) (Johnson 1903) and the others, including a more ventral pair, are quite short for a nereid.

Branchiae: Absent (Blake and Ruff 2007).

Burrow/Tube: Individuals build thin, pale brown, loosely constructed tubes in vertical burrows that are Y-shaped and mucus lined (Smith 1950). Newly hatched young build protective tubes of sand grains and mucus.

Pharynx: The pharynx bears a distinct eversible proboscis. The everted proboscis has two rings, oral (or proximal) and distal (or maxillary) and terminates with two fang-shaped jaws (Fig. 3). The oral ring is used largely in burrowing, while the distal ring is used in feeding (Barnes and Head 1977).

Each ring is equipped with many papillae and conical paragnaths and their patterns are taxonomically relevant. In this species Area I usually has one tooth; Area II has the largest teeth and about 12 in a crescent; Area III has a broad patch of 20–25; IV has broad crescents of 30–35; V usually has no paragnaths (Hartman 1938); VI has three small points and Areas VII and VIII have two continuous rows (Figs. 3a,b).

Genitalia:

Nephridia:

Possible Misidentifications

The prostomia of nereid worms are quite alike, with four eyes, a pair of frontal antennae and biarticulate palps, and 3–4 pairs of tentacular cirri. The genus *Neanthes* currently, includes 3–4 local species (Blake and Ruff 2007). *Neanthes* species have only homogomph spinigerous setae in the posterior notopodia, a trait it shares with *Hediste*, but without the fused falcigers. Some authors currently place *N. limnicola* in the genus *Hediste* (Sato 1999; Bakken and Wilson 2005; Tusuji and Sato 2012). The genus *Neanthes* is further distinguished by having only conical paragnaths on both proboscis rings, and biramous parapodia with composite setae (Hartman and Reish 1950). *Neanthes limnicola* is distinct because individuals are usually pale and translucent, not dark green and its posterior parapodial

lobes are not expanded like those of *N. brandti*.

Neanthes brandti has been at times considered a subspecies or a synonym of *N. virens*, the large (50–50 cm in length), cold-water form (Breton et al. 2004). This latter species, however, has only a few paragnaths on its proboscis rings, (i.e. 2–3 rows in Areas VII, VIII), not many as in *N. brandti* (4–5 rows in Areas VII, VIII). The prostomium of *N. virens* is small and triangular, its eyes are small and on the posterior half of the prostomium. It has short antennae and massive palps. These species exhibit overlapping geographic distributions and it is possible that they are the same species (Breton et al. 2004).

Neanthes succinea is one of the most common nereids in the NE Pacific but is recognizable from *N. brandti* by its very enlarged posterior notopodial lobes, with a small distal dorsal cirrus attached at the end of the lobe (Blake and Ruff 2007). It has a heteronereid form and *N. limnicola* does not. *N. succinea* is thought to be a more southern form (although it has been reported from Netarts Bay).

Neanthes species have spinigerous notosetae only (Hilbig 1997). The morphologically similar genus, *Nereis sensu stricto*, is characterized by species with spinigerous notosetae in the anterior half of the body and falcigerous notosetae posteriorly (Pettibone 1963; Smith 1959). Common *Nereis* species include the very abundant *Nereis vexillosa*, an olive green to brown worm found in many diverse marine environments, especially in mussel beds. It has greatly elongated, strap-like notopodial lobes in the posterior parapodia. *Nereis eakini*, from rocky habitats, has a long prostomium and proboscis rings covered with small round paragnaths. The bright green *Nereis grubei* has greatly expanded posterior notopodial parapodial lobes and no paragnaths in Area V of the proboscis. *Nereis procera* is subtidal in sand, has tiny eyes, a very long body, and unusually inconspicuous paragnaths on its proboscis (Hartman 1968). The genus *Nereis* differs from *Hediste* because members of the latter genus has 1–3 fused falcigers on the supra-acicular bunch of posterior neuropodial setae

(no local species are known, Blake and Ruff 2007).

Ecological Information

Range: Type locality is Lake Merced, California (Johnson 1903). Known range includes Salinas River, California, north to Vancouver Island, B.C. (Smith 1958).

Local Distribution: Coos Bay distribution includes sites along the South Slough estuary as well as Coos Bay, Kentuck Inlet and the Coos River mouth.

Habitat: Isolated populations occur in loose burrows in sand and clay banks. Individuals prefer soft mud, sometimes in channels with *Salicornia* (Smith 1953). However, *N. limnicola* is not limited by substrate and can survive in almost entirely dry mud. Thus, this species can survive in unstable environment (e.g. Salinas River, Smith 1953). The unique reproductive strategy (see **Reproduction**) of *N. limnicola* may have evolved in response to the unstable or extreme habitats in which they live (Tosuji et al. 2010).

Salinity: Adapts to a wide range in salinity from 2–25, but is usually found in areas of reduced salinity (Smith 1950). This species is known to inhabit brackish or freshwater (Sato 1999; Blake and Ruff 2007)

Temperature: From cool and temperate waters and, although warmth (30°C) negatively affects reproduction, it does not cause fatalities (Smith 1953).

Tidal Level: Shallow intertidal.

Associates: In the Salinas River, associates include the isopod *Gnorimosphaeroma oregonensis*, and amphipods *Corophium spinicorne*, *Anisogammarus contervicolus* (Smith 1953). *N. limnicola* does not overlap with *Nereis vexillosa* or *Neanthes brandti* (Coos Bay, 1970 unpublished student report).

Abundance: Abundant at Coos bay, especially the east side of Coos Bay (L.C. Oglesby, pers. com.). Populations are irregularly distributed and tend to occur in isolation in shallow water in Salinas River, California (Smith 1950, 1958).

Life-History Information

Reproduction: The reproduction and development of *Neanthes limnicola* (= *Neanthes lighti*) was described by Smith (1950). *N. limnicola* is a unique nereid in that individuals are viviparous, hermaphroditic and

self-fertile. Although individuals are self-fertile, genetic evidence suggests that they are capable of outcrossing to maintain genetic diversity (Fong and Garthwaite 1994).

Oocytes are approximately 120–170 µm in diameter (Sato 1999; Fernald et al. 1987) and develop within the adult coelom, by typical spiral cleavage, until they are 4–8 mm in length (20 setiger stage). Adults have been found with larvae within their coelom in July–August (Washington, Fernald et al. 1987). Breeding occurs in late winter through spring and summer, when high temperatures and salinity suppress sexual activity (Salinas River Estuary, CA, Smith 1953).

Larva: Larvae grow rapidly into ciliated trochophores. At the 20-setiger stage, larvae hatch by rupturing of the body wall of the parent (Smith 1950). Total development time ranges from 21–28 days. Newly hatched young immediately build protective tubes of sand grains and mucus.

Juvenile:

Longevity:

Growth Rate:

Food: Nereids use their jaws to tear apart and eat pieces of algae and diatomaceous detritus from the surface of the bottom (Smith 1950; Kozloff 1993).

Predators:

Behavior: Free-living and constructs a mucus-lined burrow, which is somewhat Y-shaped and deep (Kozloff 1993). Worm exists above the fork of the “Y” and can escape down into the burrow during dry periods. *N. limnicola* individuals can swim well.

Bibliography

1. BAKKEN, T., and R. S. WILSON. 2005. Phylogeny of nereidids (Polychaeta: Nereididae) with paragnaths. *Zoologica Scripta*. 34:507-547.
2. BARNES, R. S. K., and S. M. HEAD. 1977. Variation in paragnath number in some British populations of estuarine polychaete *Nereis diversicolor*. *Estuarine and Coastal Marine Science*. 5:771-781.
3. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In: The Light and Smith manual: intertidal invertebrates from central California to*

- Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
4. BRETON, S., F. DUFRESNE, G. DESROSIERS, and P. BLIER. 2004. Morphological variation in *Nereis (Neanthes) virens* (Polychaeta: Nereididae) populations. *Journal of the Marine Biological Association of the United Kingdom*. 84:983-985.
 5. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County Science Series*. 28:1-190.
 6. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 7. FONG, P. P., and R. L. GARTHWAITE. 1994. Allozyme electrophoretic analysis of the *Hediste limnicola*-*H. diversicolor*-*H. japonica* species complex (Polychaeta: Nereididae). *Marine Biology*. 118:463-470.
 8. HARTMAN, O. 1938. Brackish and fresh-water Nereidae from the Northeast Pacific, with the description of a new species from central California. University of California Press, Berkeley, California.
 9. —. 1968. Atlas of the errantiate polychaetous Annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
 10. HARTMAN, O., and D. J. REISH. 1950. The Marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
 11. HILBIG, B. 1997. Family Nereididae, p. 291-316. *In: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel*. Vol. 4. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
 12. JOHNSON, H. P. 1903. Fresh-water Nereidae from the Pacific coast and Hawaii, with remarks on freshwater Polychaeta in general. Henry Holt, New York.
 13. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
 14. PETTIBONE, M. 1963. Aphroditidae through Trochochaetidae. *In: Marine polychaete worms of the New England Region*. Vol. 1. Smithsonian Institution, Washington, D.C.
 15. SATO, M. 1999. Divergence of reproductive and developmental characteristics in *Hediste* (Polychaeta: Nereididae). *Hydrobiologia*. 402:129-143.
 16. SMITH, R. I. 1950. Embryonic development in the viviparous nereid polychaete *Neanthes lighti* Hartman. *Journal of Morphology*. 87:417-465.
 17. —. 1953. The distribution of the polychaete *Neanthes lighti* in the Salinas River estuary, California, in relation to salinity, 1948-1952. *Biological Bulletin*. 105:335-347.
 18. —. 1958. On reproductive pattern as a specific characteristic among nereid Polychaetes. *Systematic Zoology*. 7:60-73.
 19. —. 1959. The synonymy of the viviparous polychaete *Neanthes lighti* Hartman (1938) with *Nereis limnicola* Johnson (1903). *Pacific Science*. 13:349-350.
 20. TOSUJI, H., and M. SATO. 2012. A simple method to identify *Hediste* sibling species (Polychaeta: Nereididae) using multiplex PCR amplification of the mitochondrial 16S rRNA gene. *Plankton & Benthos Research*. 7:195-202.
 21. TOSUJI, H., K. TOGAMI, and J. MIYAMOTO. 2010. Karyotypic analysis of the hermaphroditic viviparous polychaete, *Hediste limnicola* (Polychaeta: Nereididae): possibility of sex chromosome degeneration. *J. Mar. Biol. Assoc. U.K.* 90:613-616.

Updated 2015

Nereis vexillosa

The large mussel worm

Phylum: Annelida
Class: Polychaeta
Order: Phyllodocida
Family: Nereidae

Taxonomy: One may find several subjective synonyms for *Nereis vexillosa*, but none are widely used currently.

Description

Size: Individuals living in gravel are larger than those on pilings and sizes range from 150–300 mm in length (Johnson 1943; Ricketts and Calvin 1971; Kozloff 1993) and up to 12 mm in width (Hartman 1968). Epitokous adults are much larger than sexually immature individuals. For example, one year old heteronereids were at least 560 mm in length (Johnson 1943).

Color: Body color grey and iridescent green, blue and red body color. Females have more a reddish posterior than males (Kozloff 1993).

General Morphology: Thick worms that are rather wide for their length (Fig. 1).

Body: More than 100 body segments are normal for this species (Hartman 1968), the illustrated specimen has 105 segments (Fig. 1). Nereids are recognizable by their anterior appendages including two prostomial palps and four peristomial tentacular cirri (see **Anterior appendages**) (Fig. 2) (Blake and Ruff 2007).

Anterior: Prostomium pyriform and widest posteriorly (Fig 2).

Trunk: Thick segments that are wider than they are long, gently tapers to posterior (Fig. 1).

Posterior: Pygidium bears a posterior cirrus with four, fine, accessory lobes (Fig. 1) that are often broken during collection.

Parapodia: Parapodia are of typical nereid biramous structure (Figs. 5, 6, 7) from the third setiger (Hilbig 1997). Posterior notopodial lobes gradually change into long strap-like ligules (Fig. 6), with dorsal cirrus inserted terminally (most important species characteristic). The parapodia of epitokous individuals are modified for swimming and are wide and plate-like (Kozloff 1993).

Setae (chaetae): Notopodia bear homogomph spinigers anteriorly (Fig. 8d) that

gradually transition to few short homogomph falcigers posteriorly (Fig. 8a). Both anterior and posterior neuropodia have homo- and heterogomph spinigers (Fig. 8c, d) and heterogomph falcigers (Fig. 8b) (*Nereis*, Hilbig 1997). Acicula, or heavy internal black spines, are found on all noto- and neuropodia (Figs. 6).

Eyes/Eyespots: Two pairs of small ocelli are present on the prostomium (Fig. 2).

Anterior Appendages: Prostomium bears two small antennae and two massive palps each with small styles. Four pairs of tentacular cirri are also present and the two dorsal pairs are longest (Fig. 2).

Branchiae: Absent (Blake and Ruff 2007).

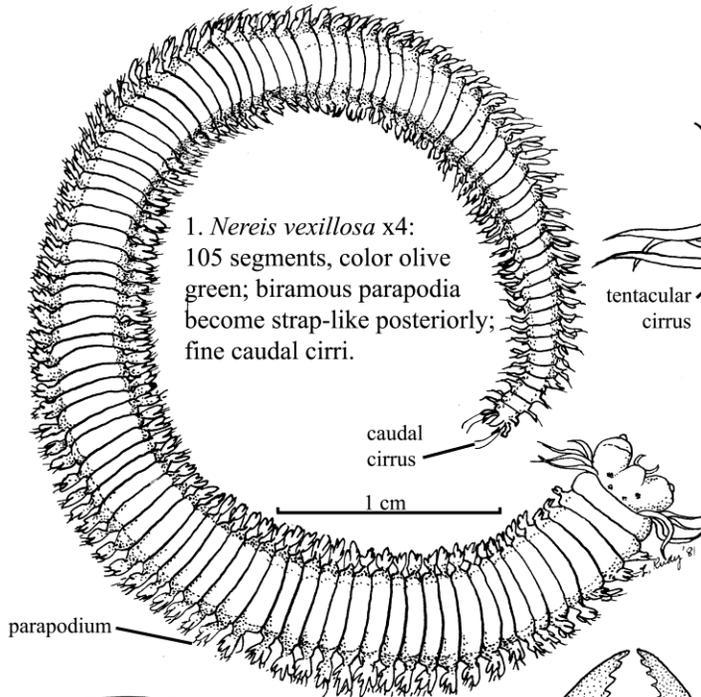
Burrow/Tube: Newly hatched animals build flimsy mucus and sand tubes (Johnson 1943). Adult worm to tube length ratio is 1.65:1 (Roe 1975).

Pharynx: The pharynx bears a distinct eversible proboscis. The everted proboscis has two rings, oral (or proximal) and distal (or maxillary) and terminates with two fang-shaped jaws, with 6–8 teeth (Fig. 3, 4). The oral ring is used largely in burrowing, while the distal ring is used in feeding (Barnes and Head 1977). Each ring is equipped with many papillae and conical paragnaths and their patterns are taxonomically relevant. Paragnaths (conical teeth) on both oral and maxillary rings are arranged as follows: Area I has several small cones in tandem; Area II has an oblique, small transverse patch (Fig. 3); Area III has a circular patch; Area IV (paired) with an oblique patch of several rows, both are ventral; Area V has no paragnaths; Area VI with a mass of 6–9 or more and both are dorsal (Fig. 3); Areas VII and VIII both have continuous bands of many paragnaths, those anterior being largest and both are ventral (Fig. 4).

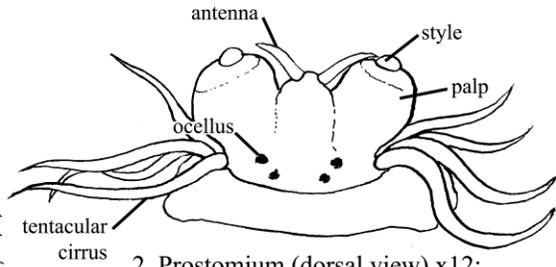
Genitalia:

Nephridia:

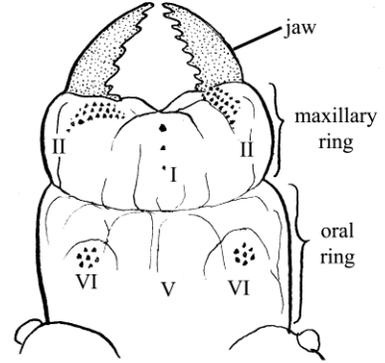
Nereis vexillosa



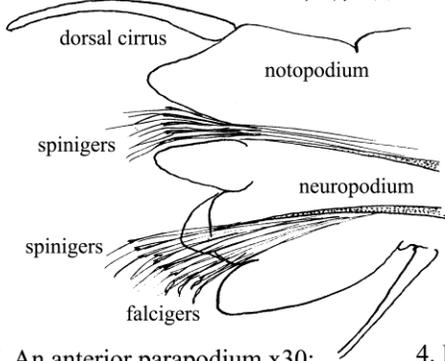
1. *Nereis vexillosa* x4:
105 segments, color olive green; biramous parapodia become strap-like posteriorly; fine caudal cirri.



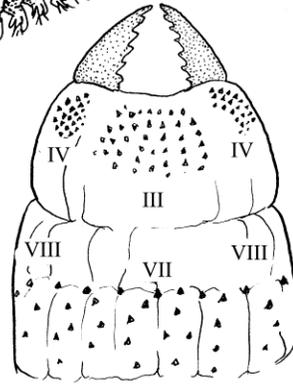
2. Prostomium (dorsal view) x12:
four small ocelli; one pair antennae; massive palps, small styles; four pairs tentacular cirri.



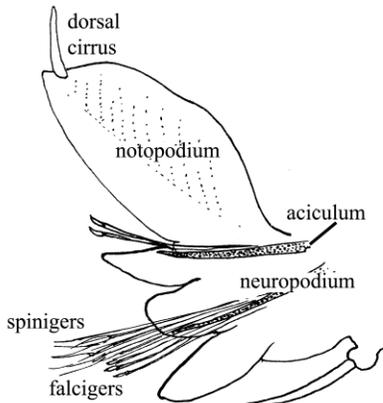
3. Everted proboscis (dorsal view) x12:
conical paragnaths, oral and maxillary rings; jaws 6-8 teeth; paragnaths area - I: several small cones in tandem, II: an oblique, small transverse patch, V: none, VI: 6-9 or more in a mass.



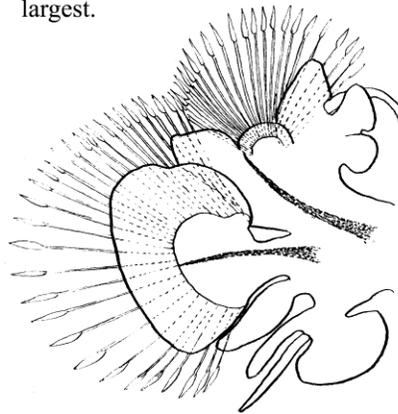
5. An anterior parapodium x30:
biramous; notopodial and neuropodial lobes 'normal', not strap-like.



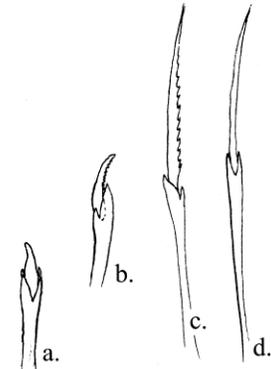
4. Everted proboscis (ventral view) x12:
paragnaths area - III: circular patch, IV: oblique patch, several rows, VII: many, continuous band, VIII: anterior cones largest.



6. A posterior parapodium x30:
notopodial lobe long, strap-like; dorsal cirrus attached terminally.



7. Heteronereia parapodium, female (Johnson, 1943).



8. Setae:
a. homogomph falciger (notopodial)
b. heterogomph falciger (neuropodial)
c. heterogomph spiniger
d. homogomph spiniger

Possible Misidentifications

The prostomia of nereid worms are quite alike, with four eyes, a pair of frontal antennae and biarticulate palps, and 3–4 pairs of tentacular cirri. Common local nereids are those in the genera *Neanthes* and *Nereis*. *Neanthes* species have only homogomph spinigerous setae in the posterior notopodia. The genus *Neanthes* is further distinguished by having only conical paragnaths on both proboscis rings, and biramous parapodia with composite setae (Hartman and Reish 1950). *Neanthes* have spinigerous notosetae only (Hilbig 1997). The morphologically similar genus, *Nereis sensu stricto*, is characterized by species with spinigerous notosetae in the anterior half of the body and falcigerous notosetae posteriorly (Smith 1959; Pettibone 1963).

Common local *Nereis* species include 6–7 species (Blake and Ruff 2007). *Nereis eakini*, from rocky habitats, that has a long prostomium and proboscis rings covered with small round paragnaths. The bright green *Nereis grubei* has greatly expanded posterior notopodial parapodial lobes and no paragnaths in area V of the proboscis. *Nereis procera* is subtidal in sand, has tiny eyes, a very long body, and unusually inconspicuous paragnaths on its proboscis (Hartman 1968). *Nereis latescens* is common amongst algal holdfasts and their dorsum bears transverse lines of brown pigment (Blake and Ruff 2007). *Nereis pelagica* is an intertidal to subtidal species with dark parapodial lobes. The common and abundant *Nereis vexillosa*, can be differentiated from the above species by its olive green to brown color where it is found in many diverse marine environments, especially in mussel beds. Furthermore, it has distinct greatly elongated, strap-like notopodial lobes in the posterior parapodia.

Other morphologically similar species include those in the genus *Neanthes*. *Neanthes limnicola* individuals are usually pale and translucent, not distinctly green as in *N. vexillosa*. *Neanthes brandti* has been at times considered a subspecies or a synonym of *N. virens*, (Breton et al. 2004) and is large, sand-dwelling and green in color like *N. vexillosa*. However, *N. brandti* is usually paler

ventrally and, in contrast to *N. vexillosa*, it has many teeth on all areas of the proboscis, its posterior parapodial lobes are leaf-like, not long and strap-like. *N. brandti* also has no falcigers in the posterior notopodia and its ecological niche is different, it does not live in mussel beds or on pilings. *Neanthes succinea* is one of the most common nereids in the Northeast Pacific and has a very enlarged posterior notopodial lobes, with a small distal dorsal cirrus attached at the end of the lobe (Blake and Ruff 2007). *N. succinea* is thought to be a more southern form (although it has been reported from Netarts Bay).

Ecological Information

Range: Type localities are Alaska and Siberia. Known range includes eastern Siberia to Alaska and south to central California (Hartman 1968).

Local Distribution: Coos Bay distribution includes many sites and, within Oregon, *N. vexillosa* has also been found in Yaquina Bay.

Habitat: Individuals occur among heavy algae cover, eelgrass, bark, and under rocks or cobblestones. Their preferred substrate is sand or mud mixed with sand. *N. vexillosa* also occurs in mussel beds and barnacle clusters on intertidal pilings along the open coast (Blake and Ruff 2007).

Salinity: *Nereis vexillosa* is strictly a marine species.

Temperature: Cold water to temperate (Johnson 1943).

Tidal Level: Intertidal and shallow water (Johnson 1943).

Associates: Occurs with *Neanthes virens*, in mussel beds and with the scaleworm *Halosydna*, porcelain crab *Petrolisthes*, and isopod *Cirolana*.

Abundance: Ubiquitous (Ricketts and Calvin 1971). The most abundant large annelid of the Pacific Northwest (Johnson 1943), but varies in abundance throughout wide geographical range (Ricketts and Calvin 1971). About 22 individuals/m² were reported in Mitchell Bay, Washington (Roe 1975).

Life-History Information

Reproduction: *Nereis vexillosa* has heteronereid a form (called an epitoke) characterized by modified parapodia (Fig. 7).

These epitokes swarm at night in summer months (June in Coos Bay and March-August in Washington, Fernald et al. 1987). Males appear first near water's surface, then females. Large (200–250 µm in diameter) oocytes are released from the females in a gelatinous mass and both female and egg mass sink to the benthos. Both adults usually die shortly thereafter (Fernald et al. 1987). Eggs are found in a firm, irregular, gelatinous mass, 2.5–7.5 cm in diameter, translucent and blue green, green or brown when freshly laid. Eggs can withstand strong wave action. *N. vexillosa* is the only nereid with a solid egg mass.

Larva: Larval development was described by Johnson (1943). Pelagic and lecithotrophic larvae hatch from the gelatinous egg mass between 3–5 setiger stages. Survivorship of larvae is reduced due to ingestion by the co-occurring terebellid polychaete *Eupolyornia heterobranchia* (Wilson 1980). When larvae are 1–2 weeks old (4–6 setiger stages), they build mucus tubes and begin to feed (Roe 1975; Fernald et al. 1987).

Juvenile: In the field, juveniles have 8–25 setigers from 3–5 weeks, are one half adult size after one year and are fully grown and sexually mature the following year (Roe 1975). Juveniles can grow quickly in the lab, on a diet of other polychaetes (Johnson 1943). In the field, they can be territorial two weeks after hatching (Roe 1975).

Researchers have shown that *N. vexillosa* is less likely to burrow into sediment that has been recently disturbed (e.g., by erosion, mixing, fresh feces, burrow trails and feeding tracks) (Woodin et al. 1995).

Longevity: Two-year life-span (Roe 1975).

Growth Rate: Varies greatly. At 4–12 months and 60 segments, adult species characteristics are conspicuous, including strap-like parapodial lobes (Johnson 1943).

Food: *N. vexillosa* is omnivorous and prefers fresh animal food, and will reject dead food. This species is not a scavenger by preference (Johnson 1943). Nereids use their jaws to tear apart and eat pieces of algae (Kozloff 1993). Young build flimsy mucus and sand tubes, and rarely leave them completely to feed.

Predators: Sometimes preyed upon by nemertean *Paranemertes peregrina* (Roe 1970). Widely used by man for fish bait.

Behavior: Very active worm that can bite human collector.

Bibliography

1. BARNES, R. S. K., and S. M. HEAD. 1977. Variation in paragnath number in some British populations of estuarine polychaete *Nereis diversicolor*. *Estuarine and Coastal Marine Science*. 5:771-781.
2. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
3. BRETON, S., F. DUFRESNE, G. DESROSIERS, and P. BLIER. 2004. Morphological variation in *Nereis (Neanthes) virens* (Polychaeta : Nereididae) populations. *Journal of the Marine Biological Association of the United Kingdom*. 84:983-985.
4. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
5. HARTMAN, O. 1968. Atlas of the errantiate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
6. HARTMAN, O., and D. J. REISH. 1950. The Marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
7. HILBIG, B. 1997. Family Nereididae, p. 291-316. *In: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel*. Vol. 4. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
8. JOHNSON, M. W. 1943. Studies on the life history of the marine annelid *Nereis vexillosa*. *Biological Bulletin*. 84:106-14.

9. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
10. PETTIBONE, M. 1963. Aphroditidae through Trochochaetidae. *In*: Marine polychaete worms of the New England Region. Vol. 1. Smithsonian Institution, Washington, D.C.
11. RICKETTS, E. F., and J. CALVIN. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
12. ROE, P. 1975. Aspects of life-history and of territorial behavior in young individuals of *Platynereis bicanaliculata* and *Nereis vexillosa* (Annelida: Polychaeta). *Pacific Science*. 29:341-348.
13. ROE, P., and R. GIBSON. 1970. The Nutrition of *Paranemertes peregrina* (Rhynchocoela: Hoplonemertea). *Biological Bulletin*. 139:80-91.
14. SMITH, R. I. 1959. The synonymy of the viviparous polychaete *Neanthes lighti* Hartman (1938) with *Nereis limnicola* Johnson (1903). *Pacific Science*. 13:349-350.
15. WILSON, W. H. 1980. A Laboratory investigation of the effect of a terebellid polychaete on the survivorship of nereid polychaete larvae. *Journal of Experimental Marine Biology and Ecology*. 46:73-80.
16. WOODIN, S. A., S. M. LINDSAY, and D. S. WETHEY. 1995. Process-specific recruitment cues in marine sedimentary systems. *Biological Bulletin*. 189:49-58.

Updated 2015

Eteone lighti

A paddleworm

Phylum: Annelida
Class: Polychaeta
Order: Phyllodocida
Family: Phyllodocidae

Taxonomy: The genus *Eteone* was revised into three genera (*Eteone*, *Hypereteone*, *Mysta*) by Wilson (1988) based on anal cirri morphology and the presence and location of proboscis papillae. Thus, *E. lighti* is sometimes referred to as *Hypereteone lighti*. While the presence of three major groups are apparent, splitting *Eteone* into these genera has not been recognized by most authors and *E. lighti* is the name most commonly seen (Pleijel 1991; Blake 1992; Blake 1997; Blake and Ruff 2007).

Description

Size: Individuals to 30 mm in length and 1–1.5 mm in width (Hartman 1968). A 25-mm long Coos Bay specimen weighed 0.17 g (wet weight, Baker et al. 1970).

Color: Pale or white, deep yellow dorsal transverse stripes (Hartman 1968) and dorsal cirri with deep yellow tips.

General Morphology: Body long and slender that gradually tapers posteriorly in the illustrated specimen (Fig. 1) and is recognizable by trapezoidal prostomium and triangular dorsal cirri (Blake and Ruff 2007).

Body: 75-100 total body segments (Fig. 1) where first segment incomplete dorsally (*Eteone*) and expands into tentacular cirri (Fig. 2a).

Anterior: Prostomium wider than long and with a median longitudinal groove (Fig. 2a). Anterior bears several paired appendages (see **Anterior appendages**) but no nuchal papilla.

Trunk:

Posterior: A single pair of cirriform anal cirri are attached laterally (Figs. 1, 5) and are approximately twice as large as tentacular cirri (Fig. 2).

Parapodia: Uniramous with neuropodia only. All but first segment with a flat triangular dorsal cirrus, about as wide as long (Fig. 3), these become longer and narrower posteriorly. The ventral cirrus has a broad base tapering to a blunt tip and is shorter than

the neuropodial lobe (Fig. 3). Note: parapodium should be examined in side view to check for flatness, inflatedness, etc.

Setae (chaetae): Setae are compound (Phyllodocidae, Blake 1975b) and consist of long, fine, colorless spinigers (Hartman 1968) (Figs. 4a,b).

Eyes/Eyespots: Two eyespots are present on posterior third of the prostomium (Fig. 2a).

Anterior Appendages: Prostomium bears two pairs of short, conical antennae and appendages on the first segment include two pairs of short and slender tentacular cirri (*Eteone*) (Fig. 2a).

Branchiae:

Burrow/Tube:

Pharynx: Pharynx bears proboscis that can be smooth or wrinkled, but lacks papillae (Hartman 1968) (Fig. 1).

Genitalia:

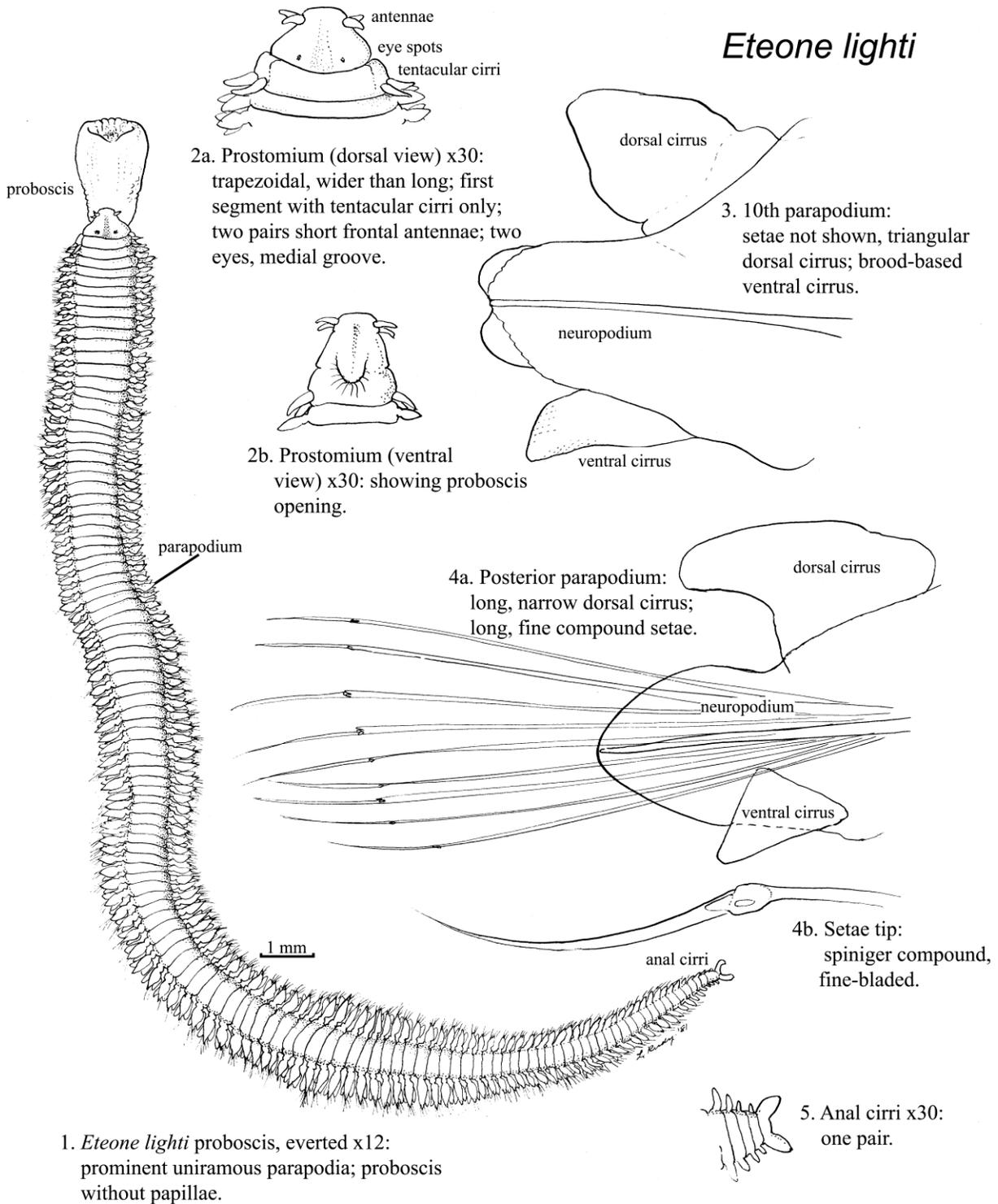
Nephridia:

Possible Misidentifications

Phyllodocids can have flattened, globular, leaf- or paddle-like parapodial cirri (Blake 1975b). The family Phyllodocidae is characterized by individuals that are long and slender and a prostomium that usually bears four antennae (and occasionally a medial one). Additionally, they have 2–4 pairs of tentacular cirri, uniramous parapodia and compound setae. Other polychaete families with similar morphology are Syllidae and Nereidae, although neither has uniramous parapodia. Phyllodocid genera are differentiable by a “tentacular formula” which combines important taxonomic characters including the arrangement of tentacular cirri, the fusion of tentaculate segments and the occurrence of setae on those segments (Blake and Ruff 2007). The genus *Eteone* has only two pairs of short tentacular cirri and short prostomial antennae (Fauchald 1977) (Fig. 2a).

The species most similar to *E. lighti* in our area is *E. pacifica*, which has no (or inconspicuous) eyes, a prostomium longer

Eteone lighti



than wide, flat broadly rounded asymmetrical dorsal cirri and irregularly spaced black spots on its yellowish body. Individuals are large and can be more than 100 mm in length (Blake and Ruff 2007). A variety, *E. p. spetsbergensis*, has parapodial setae with two large, equal teeth at the end of the shaft (*E. pacifica sensu stricto* has setae with two unequal teeth at the end of the shaft) (Banse and Hobson 1974).

Other species of *Eteone* include *E. californica*, which also has a broad truncate prostomium, but has a nuchal papilla between its dark red eyes, and wide, dorsal parapodial cirri. Its ventral cirri are very short in the posterior parapodia, it has small brown pigment spots on its body (Banse and Hobson 1974), which comprises 80-95 total segments. *E. californica* is slightly smaller than *E. lighti* at 20 mm in length, on average, and the setae in *E. californica* have a pair of large teeth with 4–5 denticles on shaft tip (Blake 1997). *E. dilatatae* is a long, slender worm with up to 250 segments and is found on sandy beaches of the outer coasts in central and southern California (Hartman 1936; Blake and Ruff 2007). *E. dilatatae* is pale green in body color and characterized by a long prostomium and sub-rectangular dorsal cirri (Blake and Ruff 2007). *E. balboaensis* is a rare and eyeless species from southern California (Hartman 1936). *E. longa*, found in the Puget Sound literature, but not in guides from California and Oregon (Blake and Ruff 2007), has a long, symmetrical conical dorsal cirrus, and a ventral cirrus almost as long as the parapodial lobe; its anal cirri are broad and spheroidal (Banse and Hobson 1974; Kozloff 1974).

Ecological Information

Range: Type locality is San Francisco Bay, California. Known range includes central and southern California extending into Oregon, but probably not to Washington (Hartman 1968; Blake and Ruff 2007).

Local Distribution: Coos Bay sites include South Slough, particularly northern sites (Porch 1970).

Habitat: Mudflats, preferring muddy sand (in Coos Bay, Porch 1970; Blake and Ruff 2007).

Salinity: Collected in Coos Bay in South Slough at salinities ranging from 20–30 (Baker et al 1970).

Temperature:

Tidal Level:

Associates: Common amongst eelgrass.

Abundance: *E. lighti* can be one of the most common and widespread mudflat worms in the upper Coos Bay. Specifically in South Slough, abundances were measured at up to several hundred individuals/m² (Porch 1970).

Life-History Information

Reproduction: Many benthic polychaetes, including phyllodocids, can reproduce via epitoky, where all or a portion of the worm transforms into a pelagic form (called an epitoke) that releases gametes (Pleijel and Rouse 2006). Reproductive modes among phyllodocids range from broadcast spawning to internal fertilization or pseudocopulation where females deposit eggs into gelatinous benthic masses. Although the reproduction and development of *E. lighti* is not known, *E. viridis* females deposit eggs (100 µm in diameter) into gelatinous masses under rocks and amongst algae, but this has not been observed in *E. longa* (eggs 80 µm in diameter) (Fernald et al. 1987; Crumrine 2001).

Larva: The development of other known *Eteone* species proceeds through trochophore and nectochaete stages where advanced larvae are large and predatory and usually collected near the bottom of plankton samples (Lacalli 1981; Fernald et al. 1987; Crumrine 2001). Of the local *Eteone* species, only the larvae of *E. longa* are known and can be identified from plankton samples (Thorson 1946; Blake 1975a; Crumrine 2001).

Juvenile: Sexual maturity in another *Eteone* species, *E. longa*, is reached at 20–30 mm in length (females reaching maturity at longer lengths) (Rasmussen 1956 in Fernald et al. 1987).

Longevity:

Growth Rate:

Food:

Predators: In Tillamook Bay, predators of *Eteone* species include *Hypomesus pretiosus* (surf smelt) in the lower bay and *Parophrys vetulus* (English Sole) in mid-bay (Forsberg et al 1977).

Behavior: *E. lighti* swim by utilizing their paddle-shaped parapodia.

Bibliography

1. BAKER, D., R. RUTOWSKI, and A. TALLMAN. 1970. Coos Bay Estuary Study Area B-4, B-5.
2. BANSE, K., and K. D. HOBSON. 1974. Benthic errantiate polychaetes of British Columbia and Washington. Fisheries and Marine Service, Ottawa, Canada.
3. BLAKE, J. A. 1975a. Phylum Annelida: Class Polychaeta, p. 151-243. *In*: Light's manual: intertidal invertebrates of the central California Coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
4. —. 1975b. The Larval development of polychaeta from the northern California Coast. III. Eighteen species of Errantia. *Ophelia*. 14:23-84.
5. —. 1992. New species and records of Phyllodocidae (Polychaeta) from the continental shelf and slope off California. *Proceedings of the Biological Society of Washington*. 105:693-708.
6. —. 1997. Family Phyllodocidae, p. 109-178. *In*: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel. Vol. 4. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
7. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In*: Light and Smith manual: intertidal invertebrates from central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.
8. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
9. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County Science Series*. 28:1-190.
10. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
11. FORSBERG, B. O., J. A. JOHNSON, and S. I. KLUG. 1977. Identification, distribution and notes on food habits of fish and shellfish in Tillamook Bay, Oregon. Oregon Department of Fish and Wildlife, s.l.
12. HARTMAN, O. 1936. A review of the Phyllodocidae (Annelida Polychaeta) of the coast of California, with descriptions of nine new species. *University of California Publications in Zoology*. 41:117-132.
13. —. 1968. Atlas of the errantiate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
14. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
15. LACALLI, T. 1981. Annual spawning cycles and planktonic larvae of benthic invertebrates from Passamaquoddy Bay, New Brunswick. *Canadian Journal of Zoology*. 59:423-440.
16. PLEIJEL, F. 1991. Phylogeny and classification of the Phyllodocidae (Polychaeta). *Zoologica Scripta*. 20:225-261.
17. PLEIJEL, F., and G. W. ROUSE. 2006. Phyllodocida, p. 431-496. *In*: Reproductive biology and phylogeny of annelida. G. W. Rouse and F. Pleijel (eds.). Science Publications, Enfield, NH.
18. PORCH, L. L. 1970. Polychaetes of Coos Bay. *In*: OIMB Unpublished Student Report, Summer 1970.
19. RASMUSSEN, E. 1956. Faunistic and biological notes on marine invertebrates. *Biologiske Meddelelser Kjobenhavn*. 23:1-84.

20. THORSON, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the sound (Oresund). Medd fra Komm Danmarks Fisk Havundersogelser Ser Plankton. 4:1-523.
21. WILSON, R. S. 1988. A Review of *Eteone* Savigny 1820, *Mysta* Malmgren 1865, and *Hypereteone* Bergstrom 1914 Polychaeta Phyllodocidae. Memoirs of the Museum of Victoria. 49:385-431.

Updated 2015

Eteone pacifica

A paddleworm

Phylum: Annelida
Class: Polychaeta
Order: Phyllodocida
Family: Phyllodocidae

Taxonomy: Treadwell described this species as *Eteone maculata* in 1922. This name was replaced by *E. pacifica* in 1936, which was later synonymized with *E. bistrata* (Hartman 1936). Some authors referred to this species under the subgenus *Mysta* (Ushakov 1955 in Banse 1972; Hartman 1936) while others (Berkeley and Berkeley 1942) recorded *E. pacifica* as a subspecies of *E. spetsbergensis*. The genus *Eteone* was revised into three genera (*Eteone*, *Hypereteone*, *Mysta*) by Wilson (1988) based on anal cirri morphology and the presence and location of proboscis papillae. While the presence of three major groups are apparent, splitting *Eteone* into these genera has not been recognized by most authors and *E. pacifica* is the name most commonly seen (Pleijel 1991; Blake 1992; Blake 1997; Blake and Ruff 2007) with synonyms including *E. maculata*, *E. Mysta bistrata*, *E. Mysta pacifica*, *E. spetsberensis pacifica* (Hartman 1936; Banse 1972).

Description

Size: Individuals to 50 to 100 mm in length and 2 to 3 mm in width (Hartman 1968; Blake and Ruff 2007).

Color: Body color is pale to bright yellow green with small black spots. Spots are round laterally and square dorsally (Blake and Ruff 2007).

General Morphology: Long and slender body with long, pointed prostomium anteriorly (Fig. 1). This species is easily recognizable by its body pigmentation.

Body: 200–300 total body segments (Fig. 1) where first segment incomplete dorsally (*Eteone*) and expands into tentacular cirri (Fig. 2).

Anterior: Prostomium definitely trapezoidal, longer than wide (Fig. 2). Anterior bears several paired appendages (see **Anterior appendages**) and minor nuchal papilla (Banse 1972).

Trunk:

Posterior: Anal appendages include one lateral pair (Fig. 1).

Parapodia: Uniramous, with short, rounded dorsal cirri (Fig. 4). Ventral cirri are narrower than dorsal, rounded and approximately the same length as parapodium.

Setae (chaetae): Setae are compound (Phyllodocidae, Blake 1975) and spinigerous with long blades and smooth shafts of unequal length (Banse 1972) (Fig. 4). Setal appendages are pointed distally (Hartman 1968).

Eyes/Eyespots: Eyes absent or inconspicuous.

Anterior Appendages: Prostomium bears two pairs of small frontal cirri. The first segment has two pairs of thick, conical, tentacular cirri, the ventral pair being the larger (Fig. 2).

Branchiae:

Burrow/Tube:

Pharynx: Pharynx bears a proboscis that is fleshy and smooth with no paragnaths (side teeth) (Fig. 3).

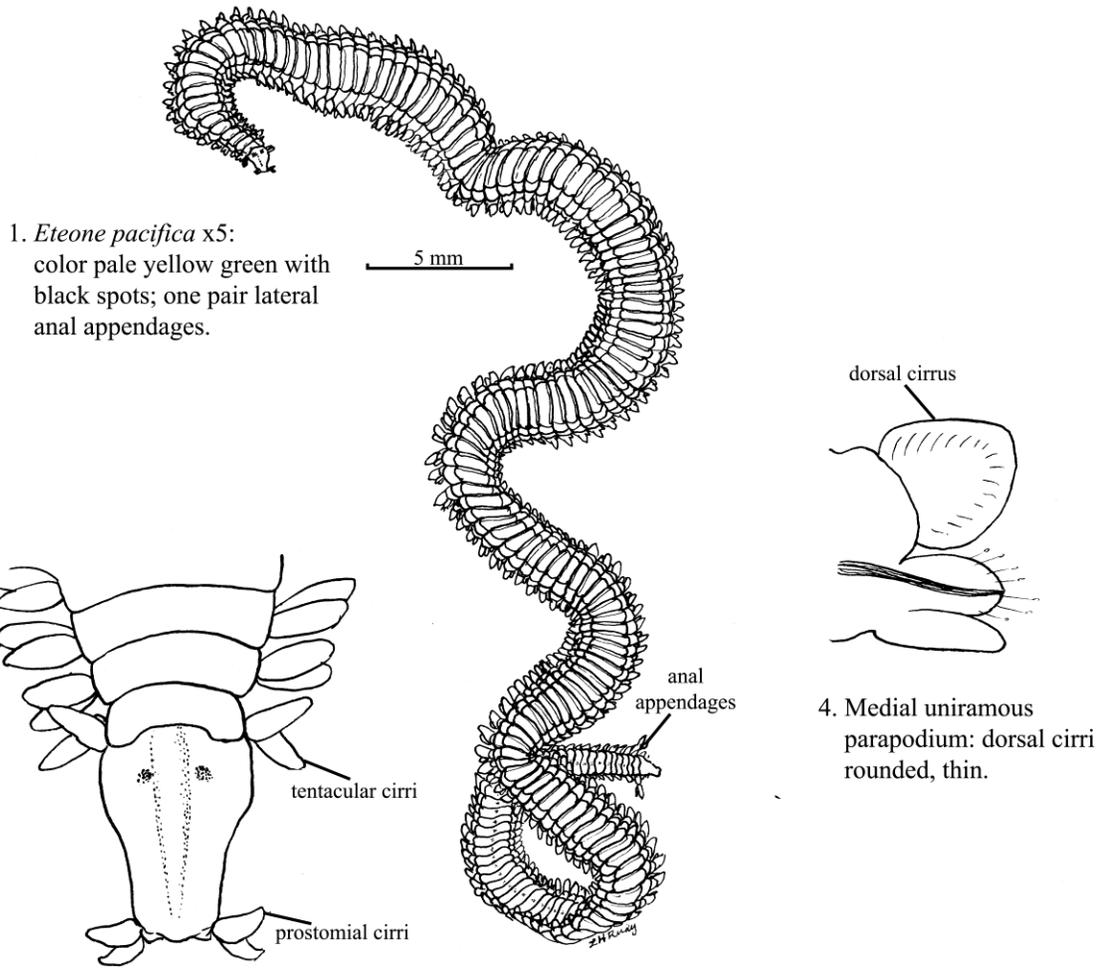
Genitalia:

Nephridia:

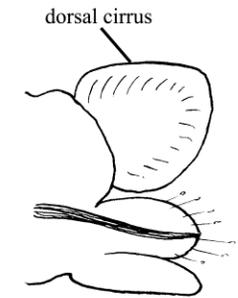
Possible Misidentifications

Phyllodocids can have flattened, globular, leaf- or paddle-like parapodial cirri (Blake 1975). The family Phyllodocidae is characterized by individuals that are long and slender and a prostomium that usually bears four antennae (and occasionally a medial one). Additionally, they have 2–4 pairs of tentacular cirri, uniramous parapodia and compound setae. Other polychaete families with similar morphology are Syllidae and Nereidae, although neither has uniramous parapodia. Phyllodocid genera are differentiable by a “tentacular formula” which combines important taxonomic characters including the arrangement of tentacular cirri, the fusion of tentaculate segments and the occurrence of setae on those segments (Blake and Ruff 2007). The genus *Eteone* has only two pairs of short tentacular cirri and

Eteone pacifica

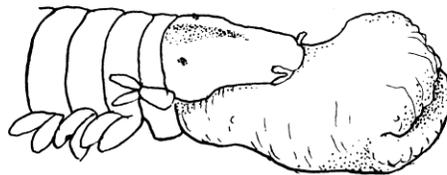


1. *Eteone pacifica* x5:
color pale yellow green with
black spots; one pair lateral
anal appendages.



4. Medial uniramous
parapodium: dorsal cirri
rounded, thin.

2. Prostomium:
two pairs of short tentacular
cirri; small eyes; two pairs
small prostomial cirri.



3. Proboscis, everted:
fleshy, smooth; no paragnaths.

short prostomial antennae (Fauchald 1977) (Fig. 2a).

Four other local species of *Eteone*, all smaller than 50 mm, differ from *E. pacifica* in several ways. The species most similar to *E. pacifica* is *E. lighti* where the latter species has two eyes and a broad trapezoidal prostomium, becoming very narrow with triangular dorsal parapodial cirri (not round). *E. lighti* body color is pale, or white.

Other species of *Eteone* include *E. californica*, which also has a broad truncate prostomium, but has a nuchal papilla between its dark red eyes, and wide, dorsal parapodial cirri. Its ventral cirri are very short in the posterior parapodia, it has small brown pigment spots on its body (Banse and Hobson 1974), which comprises 80-95 total segments. *E. californica* is slightly smaller than *E. lighti* at 20 mm in length, on average, and the setae in *E. californica* have a pair of large teeth with 4–5 denticles on shaft tip (Blake 1997). *E. dilatatae* is a long, slender worm with up to 250 segments and is found on sandy beaches of the outer coasts in central and southern California (Hartman 1936; Blake and Ruff 2007). *E. dilatatae* is pale green in body color and characterized by a long prostomium and sub-rectangular dorsal cirri (Blake and Ruff 2007). *E. balboaensis* is a rare and eyeless species from southern California (Hartman 1936). *E. longa*, is described in the Puget Sound literature, but not in guides from California and Oregon (Blake and Ruff 2007), has a long, symmetrical conical dorsal cirrus, and a ventral cirrus almost as long as the parapodial lobe; its anal cirri are broad and spheroidal (Banse and Hobson 1974; Kozloff 1974).

Ecological Information

Range: Type locality is Washington state (Hartman 1968). Known range includes western Canada to central California.

Local Distribution: Coos Bay collection sites in South Slough and outer shore, including Cape Arago and Sunset Bay (Hartman and Reish 1950).

Habitat: Intertidal muddy sand at littoral depths (Hartman 1968). *E. pacifica* is common in large muddy areas, upper Coos Bay (Porch 1970).

Salinity: *E. pacifica* was collected in Coos Bay where surface water salinity varies from 10–30.

Temperature: Surface water temperature where *E. pacifica* was collected in Coos Bay varies from 8–18 °C.

Tidal Level: Individuals collected at about +1.2 m tidal elevation in Coos Bay.

Associates: Other polychaetes, as well as the tanaidacean, *Leptocheilia dubia*, the amphipod, *Corophium brevis*, and clam, *Macoma* sp. (in South Slough).

Abundance: High abundances in Coos Bay were several hundred individuals/m² (Berkeley and Berkeley 1948)

Life-History Information

Reproduction: Many benthic polychaetes, including phyllodocids, can reproduce via epitoky, where all or a portion of the worm transforms into a pelagic form (called an epitoke) that releases gametes (Pleijel and Rouse 2006). Reproductive modes among phyllodocids range from broadcast spawning to internal fertilization or pseudocopulation where females deposit eggs into gelatinous benthic masses. Although the reproduction and development of *E. lighti* is not known, *E. viridis* females deposit eggs (100 µm in diameter) into gelatinous masses under rocks and amongst algae, but this has not been observed in *E. longa* (eggs 80 µm in diameter) (Fernald et al. 1987; Crumrine 2001).

Larva: The development of other known *Eteone* species proceeds through trochophore and nectochaete stages where advanced larvae are large and predatory and usually collected near the bottom of plankton samples (Lacalli 1981; Fernald et al. 1987; Crumrine 2001). Of the local *Eteone* species, only the larvae of *E. longa* are known and can be identified from plankton samples (Thorson 1946; Blake 1975; Crumrine 2001).

Juvenile: Sexual maturity in another *Eteone* species, *E. longa*, is reached at 20–30 mm in length (females reaching maturity at longer lengths) (Rasmussen 1956).

Longevity:

Growth Rate:

Food:

Predators: In Tillamook Bay, predators of *Eteone* species include *Hypomesus pretiosus* (surf smelt) in the lower bay and *Parophrys*

vetulus (English Sole) in mid-bay (Forsberg et al 1977).

Behavior: *E. pacifica* likely swim by utilizing their paddle-shaped parapodia, as do other paddle worms.

Bibliography

1. BANSE, K. 1972. On some species of Phyllodocidae, Syllidae, Nephtyidae, Gonioididae, Apistobranchidae, and Spionidae, (Polychaeta) from the northeast Pacific Ocean. *Pacific Science*. 26:191-222.
2. BANSE, K., and K. D. HOBSON. 1974. Benthic errantiate polychaetes of British Columbia and Washington. Fisheries and Marine Service, Ottawa, Canada.
3. BERKELEY, E., and C. BERKELEY. 1942. North Pacific polychaeta, chiefly from the west coast of Vancouver Island, Alaska, and Bering Sea. *Canadian Journal of Research*. 20:183-208.
4. —. 1948. Annelida. Polychaeta Errantia (Part 9). *In: Canadian Pacific fauna*. University of Toronto Press for the Fisheries Research Board of Canada, Toronto.
5. BLAKE, J. A. 1975. The Larval development of Polychaeta from the northern California Coast. III. Eighteen species of Errantia. *Ophelia*. 14:23-84.
6. —. 1992. New species and records of Phyllodocidae (Polychaeta) from the continental shelf and slope off California. *Proceedings of the Biological Society of Washington*. 105:693-708.
7. —. 1997. Family Phyllodocidae, p. 109-178. *In: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel*. Vol. 4, The Annelida, Part 2. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara.
8. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. Carlton (ed.). University of California Press, Berkeley, CA.
9. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
10. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County Science Series*. 28:1-190.
11. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
12. FORSBERG, B. O., J. A. JOHNSON, and S. I. KLUG. 1977. Identification, distribution and notes on food habits of fish and shellfish in Tillamook Bay, Oregon. Oregon Department of Fish and Wildlife, s.l.
13. HARTMAN, O. 1936. A review of the Phyllodocidae (Annelida Polychaeta) of the coast of California, with descriptions of nine new species. *University of California Publications in Zoology*. 41:117-132.
14. —. 1968. Atlas of the errantiate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
15. HARTMAN, O., and D. J. REISH. 1950. The Marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
16. KOZLOFF, E. N. 1974. Keys to the Marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
17. LACALLI, T. 1981. Annual spawning cycles and planktonic larvae of benthic invertebrates from Passamaquoddy Bay, New Brunswick. *Canadian Journal of Zoology*. 59:423-440.
18. PLEIJEL, F. 1991. Phylogeny and classification of the Phyllodocidae (Polychaeta). *Zoologica Scripta*. 20:225-261.

19. PLEIJEL, F., and G. W. ROUSE. 2006. Phyllodocida, p. 431-496. *In*: Reproductive biology and phylogeny of annelida. G. W. Rouse and F. Pleijel (eds.). Science Publications, Enfield, NH.
20. PORCH, L. L. 1970. Polychaetes of Coos Bay. *In*: OIMB Unpublished Student Report, Summer 1970.
21. RASMUSSEN, E. 1956. Faunistic and biological notes on marine invertebrates. Biologiske Meddelelser Kjobenhavn. 23:1-84.
22. THORSON, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the sound (Oresund). Medd fra Komm Danmarks Fisk Havundersogelser Ser Plankton. 4:1-523.

Updated 2015

Halosydna brevisetosa

Phylum: Annelida
Class: Polychaeta
Order: Phyllodocida
Family: Polynoidae

Taxonomy: Eastern Pacific polynoids are often reported with wide distributions resulting in numerous synonymies. Although other synonyms are reported, the most common and recent for *H. brevisetosa* is *H. johnsoni*. These two species have overlapping ranges centrally, but the range of *H. brevisetosa* extends more northerly into colder waters while *H. johnsoni* is more common in warmer, southern regions. The variation in setal morphology between them was once believed to be temperature-induced and they were synonymized (Gaffney 1973). However, after analyzing type material from both species, Salazar-Silva (2013) determined that the two are different species based on the morphology of neurosetae and re-described them.

Description

Size: Average size range is 40 to 100 mm in length (Hartman 1968). The illustrated specimen was 22 mm in length. Most scale worms are less than a few centimeters long, however, commensal specimens can be larger than free-living (Haderlie 1980; Ruff 1993).

Color: Variable body color. This specimen had mottled brown scales, with black and white spots.

General Morphology: Short worms, dorso-ventrally flattened with scale-like plates (see **Elytra**) dorsally (Polynoidae, Ruff 1993).

Body: Thin body that is sub-rectangular with 36 total segments (Salazar-Silva 2013). Body widest medially, tapering at both anterior and posterior ends (Fig. 1).

Anterior: Prostomium bilobed and most broad at posterior (Fig. 2).

Trunk:

Posterior: Posterior three segments with dorsal cirri. Pygidium bears one pair of anal cirri and anus is dorsal and between segments 35–36 (Salazar-Silva 2013).

Parapodia: Biramous. Notopodia smaller than neuropodia (Fig. 3). Neuropodia with

rounded lobe near tip of acicula. Dorsal cirri expanded distally with filiform tip and ventral cirri are short, with fine tip (Salazar-Silva 2013).

Setae (chaetae): All setae simple.

Notosetae short and serrate. Neorsetae falcate, with rows of spines toward the tips, which are entire. Neurosetae more abundant than notosetae (Fig. 3) (Salazar-Silva 2013).

Eyes/Eyespots: Two pairs of eyes present at posterior prostomium (Fig. 2).

Anterior Appendages: Three anterior antennae (Fig. 2) and two palps (*Halosynda*, Salazar-Silva 2013).

Branchiae:

Burrow/Tube:

Pharynx: Proboscis strongly developed, with four jaws and nine pairs of papillae (Salazar-Silva 2013).

Genitalia:

Nephridia:

Polynoidae-specific character

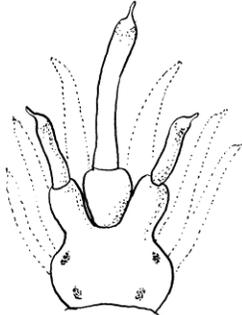
Elytra: 18 pairs occurring on segments 2–33 (segments 2, 4, 5–27 on every odd segment, and 28, 30, 31, 33) (Fig. 1). Elytra morphology is reniform to ovate, varied in color, and with a few tubercles.

Possible Misidentifications

The number of pairs of elytra make identification easy among polynoids. The 21 currently accepted *Halosydna* species worldwide are characterized by possessing 36 segments and 18 pairs of elytra (Hartman 1938). The genera most similar to *Halosydna* are *Harmothoe*, *Lepidathenia*, and *Arctonoe*, but only *Halosydna* species have 18 pairs of elytra (Ruff 1993). For example, *Harmothoe*, a closely related genus, has only 15 pairs of elytra (Barnich and Feige 2009).

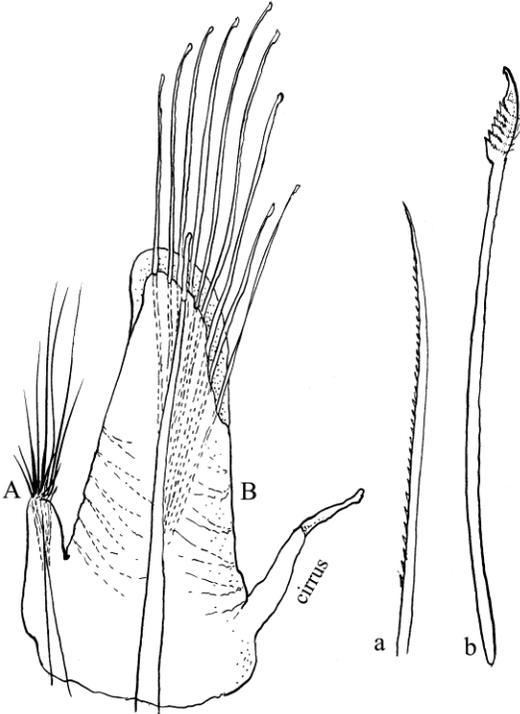
Species differentiation is usually by elytra morphology (Salazar-Silva 2010; Salazar-Silva 2013). *H. johnsoni*, a southern California species, has been confused with *H. brevisetosa* in the past. The difference between these two species is that *H.*

Halosydna brevisetosa

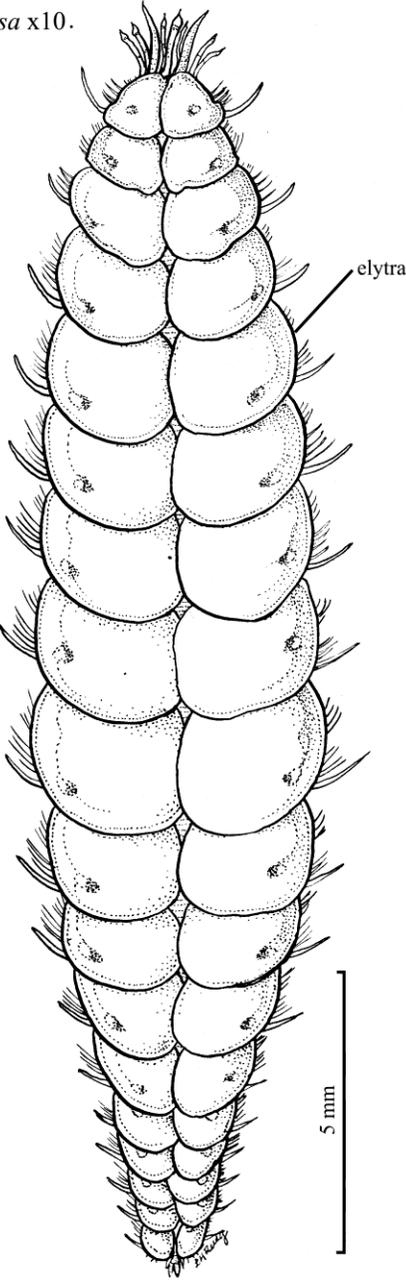


1. *Halosydna brevisetosa* x10.

2. Prostomium:
 broadest behind four eyes;
 central frontal antenna;
 antennae attached terminally
 (Hartman, 1968, p.63).



3. Parapodia:
 notopodia small, with short, serrate setae (A,a);
 neuropodia large; simple falcate setae (B,b).



brevisetosa has elytra with fringed marginal papillae that are absent in *H. johnsoni* (mid-body and posterior). Furthermore, the neurosetae in *H. brevisetosa* are complete rather than bidentate as in *H. johnsoni* (Salazar-Silva 2006; Salazar-Silva 2013). Other species of the genus *Halosydna* do not occur in the Northwest.

Ecological Information

Range: Type locality is Sausalito, San Francisco, California. Known range includes southern California to Alaska.

Local Distribution: Very common at sites in South Slough (Hartman and Reish 1950).

Habitat: Free-living individuals are found on or under rocks, pilings, and amongst mussel beds. *H. brevisetosa* also occur commensally with a variety of invertebrates (see

Associates).

Salinity:

Temperature:

Tidal Level: Intertidal. Individuals collected at a tidal elevation of 0.15 m above the mean tide level in South Slough.

Associates: Commensal individuals occur with mud-dwelling species such as hermit crabs (*Paguristes*), moon snails (*Polinices*) and other polychaetes (e.g., *Pista pacifica*, observed in South Slough), *Amphitrite robusta*, *Thelepus crispus*, *Eupolymnia heterobranchia*) (McGinitie and McGinitie 1949; Fernald et al. 1987). Prefers clean waters and seldom occurs where dissolved oxygen levels drop below 2.5 mg/l (Haderlie 1980). Commensal individuals are not chemically attracted, but possibly exhibit a tactile response to the host (Davenport and Hickok 1950).

Abundance: Most common scaleworm in central, northern California (Blake and Ruff 2007) and also very abundant in Oregon and Washington.

Life-History Information

Reproduction: Dioecious with external fertilization (Ruff 1993). Gonads in segments 12–34. In Tomales Bay, California, ripe adults were observed in August and the larvae of *H. brevisetosa* are most common in plankton samples in the late summer months (Blake 1975).

Larva: Trochophore larvae were described from wild-caught individuals by Blake (1975)

and are recognizable by a wide (400 μm) and flattened episphere, anterior to the prototroch (Crumrine 2001). They have two pairs of eyes and a small apical tuft at the anterior end. A ciliated neurotroch, which extends from the prototroch to the larval posterior, originates near the mouth. Also near the mouth, on the left side is a large tuft of long cilia. Early and late *H. brevisetosa* metatrochophores lack a telotroch. Black pigment can be observed in random patches near the prototroch and episphere. Late metatrochophores, 550 μm in length, have five pairs of elytra and three pairs of eyes (Blake 1975).

Juvenile: Young juveniles are 900 μm in length, with 11 setigerous segments, six pairs of elytra, all anterior appendages, two pairs of eyes and anal cirri (Fig. 2, Blake 1975).

Longevity:

Growth Rate:

Food: Voracious eaters (cannibals in captivity) and individuals may share host food when commensal.

Predators:

Behavior:

Bibliography

1. BARNICH, R., and D. FIEGE. 2009. Revision of the genus *Harmothoe* Kinberg, 1856 (Polychaeta: Polynoidae) in the Northeast Atlantic. *Zootaxa*: 1-76.
2. BLAKE, J. A. 1975. The larval development of polychaeta from the Northern California USA coast: Part 3, 18 species of Errantia. *Ophelia*. 14:23-84.
3. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
4. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
5. DAVENPORT, D., and J. F. HICKOK. 1950. Studies in the physiology of commensalism, II: The polynoid

- genera *Arctonoe* and *Halosydna*.
Biological Bulletin. 100:71-83.
6. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In*: Reproduction and development of marine invertebrates of the northern Pacific. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 7. GAFFNEY, P. M. 1973. Setal variation in *Halosydna brevisetosa*, a polynoid polychaeta. Systematic Zoology. 22:171-175.
 8. HADERLIE, E. C. 1980. Polychaeta: the marine annelid worms, p. 448-489. *In*: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
 9. HARTMAN, O. 1938. The types of the polychaete worms of the families Polynoidae and Polyodontidae in the United States National Museum and the description of a new genus. Proceedings of the United States National Museum. 86:107-134.
 10. —. 1968. Atlas of the errantiate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
 11. HARTMAN, O., and D. J. REISH. 1950. The Marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
 12. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 13. RUFF, R. E. 1995. Family Polynoidae Malmgren, 1867, p. 105-166. *In*: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 5. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
 14. SALAZAR-SILVA, P. 2006. Scaleworms (Polychaeta: Polynoidae) from the Mexican Pacific and some other eastern Pacific sites. Investigaciones Marinas Universidad Catolica de Valparaiso. 34:143-161.
 15. —. 2010. Redescription of *Harmothoe crucis* (Annelida, Polychaeta, Polynoidae), and re-establishment of synonymized species from the Grand Caribbean with descriptions of four new species. Marine Biology Research. 6:125-154.
 16. —. 2013. Revision of *Halosydna* Kinberg, 1856 (Annelida: Polychaeta: Polynoidae) from the Tropical Eastern Pacific and Grand Caribbean with descriptions of new species. Journal of Natural History. 47:1177-1242.

Updated 2015

Hesperonoe complanata

A commensal scale worm

Phylum: Annelida
Class: Polychaeta
Order: Phyllodocida
Family: Polynoidae

Taxonomy: Eastern Pacific polynoids are often reported with wide distributions resulting in numerous synonymies. Subjective synonyms for *Hesperonoe complanata* include *H. senilis*, determined to be the same species by Hartman (1938). *H. complanata* was also previously considered a member of the closely related genus *Harmothoe* by some authors (e.g., *Harmothoe complanata*, *H. johnsoni*), but is now recognized as *Hesperonoe complanata* based on noto- and neuropodia setal morphology (Ruff 1993; Blake and Ruff 2007).

Description

Size: Individuals up to 21 mm in length and 6 mm in width (including setae) (Johnson 1901; Hartman 1968). The illustrate specimen was approximately 12 mm in length (Fig. 1). Most scale worms are less than a few centimeters long, however, commensal specimens can be larger than free-living (Haderlie 1980; Ruff 1993).

Color: Body color bright orange-yellow with reddish color around head, elytra pale or translucent and setae clear (Hartman 1968; Blake and Ruff 2007).

General Morphology: Short worms are dorso-ventrally flattened and have scale-like plates (see **Elytra**) dorsally (Polynoidae, Ruff 1993).

Body: 36–38 total body segments.

Anterior: Prostomium six-sided, as long as wide, and deeply incised (Fig. 2). Prostomium bears many appendages (see **Anterior Appendages**).

Trunk:

Posterior:

Parapodia: Biramous with distinct noto- and neuropodia. Notopodia short, with two kinds of simple setae and a long dorsal cirrus, that is easily detached (Fig. 1, 5), and alternate with elytra (Fig. 1). Neuropodia long, with one kind of long setae (although lower ones can be thicker than upper ones) (Fauchald 1977). Ventral cirrus present (Fig. 5).

Setae (chaetae): Notosetae consists of two kinds: 1) upper are thick, stout, blunt, minutely serrated, both short and long (Fig. 5, 6a); 2) a few (4–5) slender, pointed and serrate (*Hesperonoe*, Fig. 5, 6b) (Fauchald 1977; Ruff 1993). Neurosetae (one kind) are curved, simple, and with lateral serrations (Fig. 5, 7), although upper neurosetae can be more slender, lower ones stouter (Ruff 1993).

Eyes/Eyespots: Four eyes, where each pair is arranged anterior to posterior and the anteriormost pair extends into the bilobed prostomium (Fig. 2).

Anterior Appendages: Large medial antenna and two small prostomial biarticulate antennae (inserted below lateral lobes of prostomium) (Fig. 3). Additional anterior appendages include one pair of lateral palps, which are longer than the medial antenna and red in color, and two pairs of tentacular cirri (Fig. 2, 3).

Branchiae:

Burrow/Tube:

Pharynx:

Genitalia:

Nephridia:

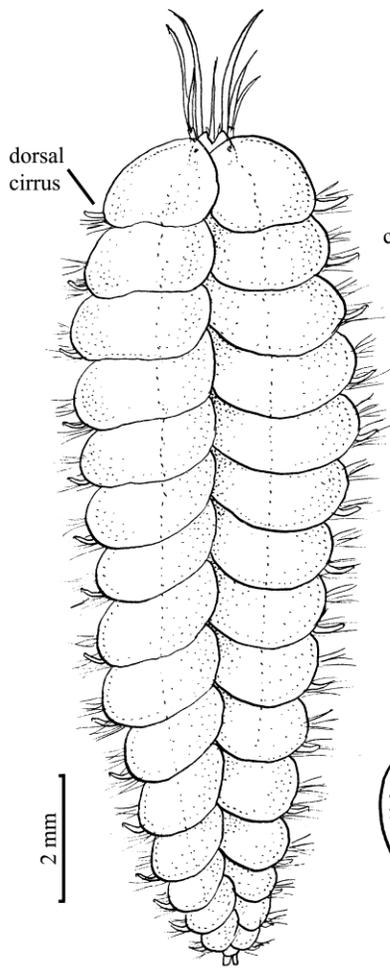
Polynoidae-specific character

Elytra: 15 pairs, reniform (kidney-shaped) (Hartman 1968), covering most of body on segments 2, 4, 5, 7, ...23, 26, 29, and 32 (Ruff 1993). Thin, delicate easily detached; with widely spaced low papillae (Fig. 4). Species with relatively smooth elytra, like this one, are often commensal (Fauchald 1977).

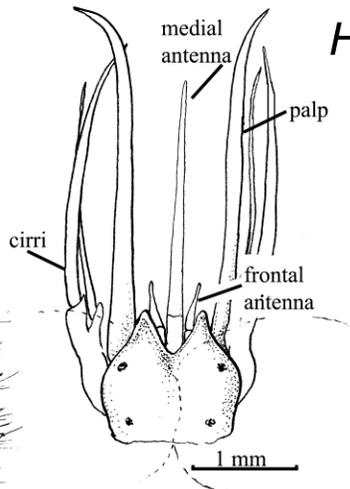
Possible Misidentifications

The number of pairs of elytra make identification easy among polynoids. The genus *Hesperonoe* can be distinguished from other polynoids by its 15 pairs of smooth elytra covering almost the entire body as well as by its prostomial antennae that are inserted ventrally, not terminally (Fig. 3), and by the possession of two kinds of simple notosetae.

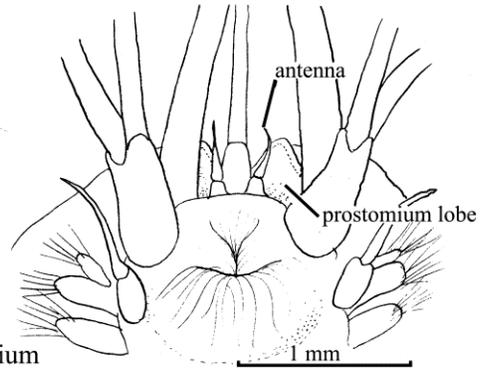
Hesperonoe complanata



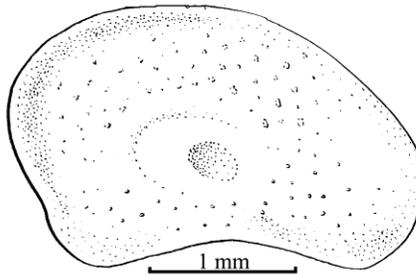
1. *Hesperonoe complanata* x11:
15 pairs smooth elytra; body flattened;
dorsal cirri alternate with elytra.



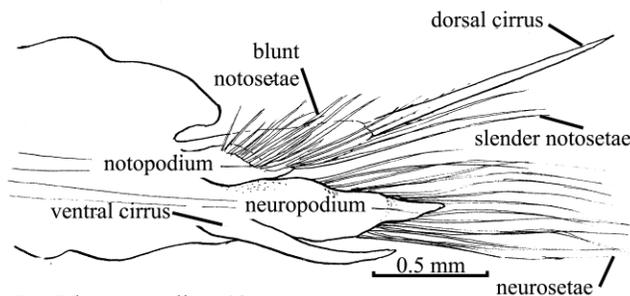
2. Head (dorsal view) x18:
two pairs of eyes; prostomium
deeply incised; short frontal
antennae, long medial one; one
pair palps, two pairs tentacular
cirri.



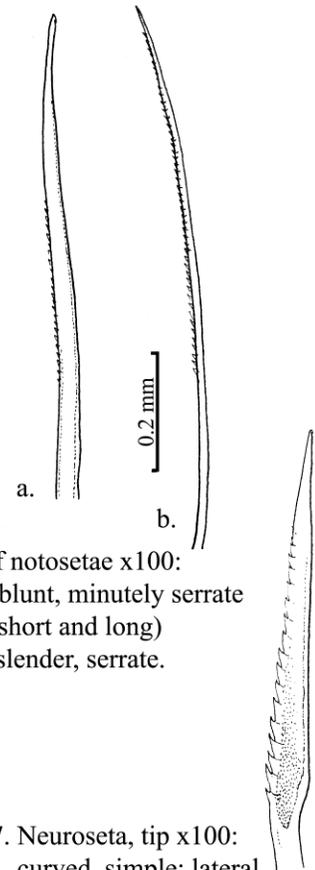
3. Head (ventral view) x30:
antennae inserted ventral to
prostomium, not terminal.



4. Elytron x25



5. 17th parapodia x40:
notopodia short, notosetae of two kinds- many stout, blunt
serrate; a few slender, pointed; serrate. Neuropodia long,
neurosetae long, slender, serrate; dorsal and ventral cirrus.



6. Ends of notosetae x100:
a. stout, blunt, minutely serrate
(both short and long)
b. long, slender, serrate.

7. Neuroseta, tip x100:
curved, simple; lateral
serrations.

Hesperonoe complanata is the only scale worm known to be commensal with the ghost shrimp *Neotrypea californiensis* and *Urechis caupo* (Blake and Ruff 2007). Another species, *H. adventor*, also lives with the echiuran, *Urechis caupo*, as well as *Upogebia pugettensis*. *H. adventor* is larger (to 40 mm), has short, ciliated palps, antennae, and dorsal cirri. Furthermore, its roundish elytra have dark crescents on their posterior thirds. The third Pacific species, *H. laevis*, is found in deep water off Santa Barbara, California, in burrows of the same echiuran listed above (Ruff 1993).

Other local polynoid genera include, *Arctonoe* and *Lepidasthenia*, each with 20 or more elytra pairs and *Halosydna* with 18 pairs of elytra. Members of the genera *Arctonoe* and *Lepidasthenia* are free-living and commensal, but individuals continue to grow segments with age, usually having more than 50 segments, not 36–38. *Hesperonoe* is similar to the local polynoid genus *Harmothoe*, as members of both genera have 15 pairs of elytra (Barnich and Feige 2009) however members of the former genus have two different kinds of setae on the noto- and neuropodia (Ruff 1993).

Ecological Information

Range: Type locality is Puget Sound, Washington. Known range includes western Canada to southern California (Hartman and Reish 1950; Hartman 1968).

Local Distribution: Local collection sites include Coos Bay estuaries. Also occurs in many *Neotrypea* burrows in larger Oregon estuaries, including Alsea, Nestucca, Netarts, Umpqua, Tillamook, and Yaquina.

Habitat: The permanent burrows and side tunnels of the ghost shrimp *Neotrypea*. They occur in the sandy mud of low intertidal mudflats in extensive beds and also among oyster beds. Juvenile *Hesperonoe* are found lying on the abdomens of *Neotrypea*, but the adults are free-living in the burrow (MacGinitie and MacGinitie 1949).

Salinity: Collected at salinities of 30 in Coos Bay and 27 in southern Puget Sound (R. Boomer pers. com.).

Temperature: Range indicates high temperature tolerance from cold temperate to warm temperate.

Tidal Level: Intertidal to upper mid-intertidal where *Neotrypea* occurs (Ricketts and Calvin 1971).

Associates: Commensal associates of *H. complanata* include those of *Neotrypea*, such as the pea crabs *Scleroplax* and *Pinnixa*, copepods *Hemicyclops* and *Clausidium*, the goby *Clevelandia*, the shrimp *Betaus* (in southern distribution), and the clam *Cryptomya* with mud shrimp *Upogebia* in California.

Abundance: MacGinitie found them in one fifth of *Neotrypea* burrows, but thought some might have escaped detection. Usually, only one adult occurs in a burrow with no other resident polychaete (MacGinitie and MacGinitie 1949).

Life-History Information

Reproduction: The reproduction and development of *H. complanata* is not known. Most polynoids have free-spawn gametes, although some brood embryos beneath their elytra (Wilson 1991; Fernald et al. 1987). Of those free-spawners, egg sizes range from 60–100 μm (Fernald et al. 1987)

Larva: The larvae of five other local polynoid species are known but not that of *H. complanata* (Crumrine 2001). Larval development most likely proceeds as planktotrophic cone-shaped trochophores and metatrochophores. In many larvae, distinct characters include a flattened episphere, distinct prototroch, up to three pairs of eyes, a conspicuous mouth posterior to the prototroch and a bundle of long cilia on the left side of the mouth (see *Halosydna brevisetosa*). These larvae can have long pelagic duration, ultimately elongating into nectochaete larvae before settlement (Lacalli 1980; Fernald et al. 1987).

Juvenile:

Longevity:

Growth Rate:

Food: Eats particles brought in by the current or trapped in *Neotrypea* burrow. Occasionally, it nibbles on the mucus lining of the burrow as well, making it parasitic, not just commensal (MacGinitie and MacGinitie 1949).

Predators:

Behavior:

Bibliography

1. BARNICH, R., and D. FIEGE. 2009. Revision of the genus *Harmothoe* Kinberg, 1856 (Polychaeta: Polynoidae) in the Northeast Atlantic. *Zootaxa*:1-76.
2. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
3. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
4. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County Science Series*. 28:1-190.
5. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
6. HADERLIE, E. C. 1980. Polychaeta: The Marine annelid worms, p. 448-489. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
7. HARTMAN, O. 1938. The types of the polychaete worms of the families Polynoidae and Polyodontidae in the United States National Museum and the description of a new genus. *Proceedings of the United States National Museum*. 86:107-134.
8. —. 1968. Atlas of the errantiate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
9. HARTMAN, O., and D. J. REISH. 1950. The Marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
10. JOHNSON, H. P. 1901. The Polychaeta of the Puget Sound region. *Boston Society of Natural History*. 29:381-437.
11. LACALLI, T. C. 1980. A guide to the marine flora and fauna of the Bay of Fundy: polychaete larvae from Passamaquoddy Bay. *Canadian Technical Report of Fisheries and Aquatic Sciences*. 940:1-27.
12. MACGINITIE, G. E., and N. MACGINITIE. 1949. *Natural history of marine animals*. McGraw-Hill Book Co., New York.
13. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
14. RUFF, R. E. 1995. Family Polynoidae Malmgren, 1867, p. 105-166. *In: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel*. Vol. 5. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
15. WILSON, W. H. 1991. Sexual reproductive modes in polychaetes: classification and diversity. *Bulletin of Marine Science*. 48:500-516.

Updated 2015

Eudistylia vancouveri

A feather-duster worm

Phylum: Annelida
Class: Polychaeta
Order: Canalipalpata, Sabellida
Family: Sabellidae, Sabellinae

Taxonomy: *Eudistylia polymorpha* was originally described as *Sabella vancouveri* and later re-described and figured by Johnson (1901) as *Bispira polymorpha*, when *Eudistylia* was differentiated by characters of thoracic notosetae which were later deemed insignificant at the genus level and the two genera were synonymized to *Eudistylia* (Fauvel 1927 and Johansson 1927 in Banse 1979). Since then, several species have been synonymized with *E. polymorpha* including *Sabella vancouveri* and *S. columbiana*, *E. abbreviata*, *E. gigantea*, *E. plumosa* and *E. tenella* (Banse 1979).

Description

Size: One of the largest sabellids. Individuals range in size from 300–480 mm in length and 15–20 mm in width, where the tube is up to 10 mm diameter (Hartman 1969; Kozloff 1974). This description is based on illustrated and dissected specimens (Fig. 1).

Color: Crown of tentacles dark red and green and radially striped (5–8 stripes) (Hartman 1969; Kozloff 1974). Hartman (1969) reports tentacles that were dark red and orange or yellow in California, but this description may refer to *E. polymorpha*, in part (see **possible misidentifications**). Some tentacles are white-tipped. The illustrated specimen (Fig. 1) had a buff colored body with light green markings and white spots. The tube is buff or grey in color.

General Morphology: A robust worm with a short tentacular crown that is brilliantly colored (Hartman 1969). Worms can be recognized in large groups called hummocks where tubes are built upon each other and resemble shrubs (e.g. Fig. 3).

Body: Body divided into thoracic and abdominal regions where abdomen gradually tapers posteriorly.

Anterior: Prostomium or head is reduced and indistinguishable (Figs. 4, 5).

Trunk: Thorax of eight segments and abdomen of many segments. Thoracic collar with four lobes (Fig. 4) that are visible on the ventral side with no long thoracic membrane. Collar is used to build the tube by incorporating sand grains with exuded mucus and attaching a “rope” to the tube anterior.

Posterior: Worm body tapers toward posterior to slender yet broad pygidium (Fig. 1).

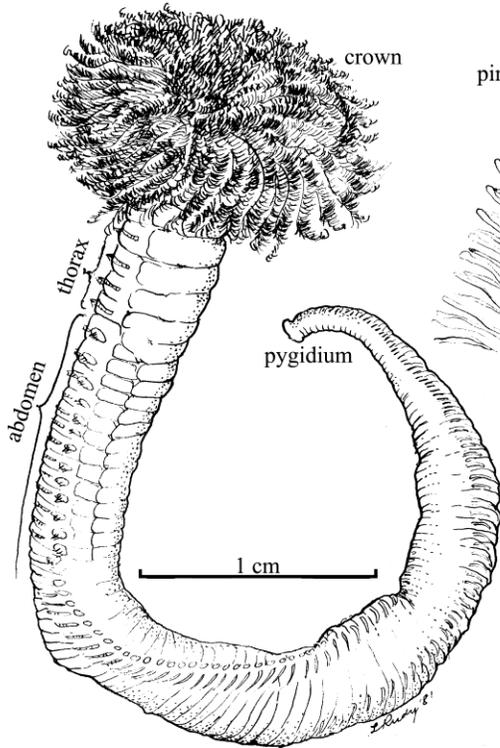
Parapodia: Biramous, (Figs. 1, 6) except for first or collar segment, which has only notopodia (Hartman 1969). In thoracic setigers (setigers 2–8), the notopodia have bundles of long and slender setae (Figs. 7b, c). The neuropodia on setigers 2–8 have pairs of short uncini (hooks) (Fig. 7a) encased in zipper-like, raised ridges called tori (Fig. 6). This arrangement is reversed in the abdomen, where the notopodia contain hooks in the abdominal segments and the neuropodia have long spines (Fig. 6).

Setae (chaetae): Thoracic notosetae of two kinds (genus *Eudistylia*): one long, slender and bilimbate (Fig. 7b) and the other spatulate and not scimitar-like (Fig. 7c). Abdominal notosetae are short avicular uncini (Fig. 7e). Thoracic neurosetae in torus, pennoned or flagged and avicular hooks or uncini arranged in a long row of about 20 pairs (Fig. 7a). Abdominal neurosetae long and pointed (Fig. 7d).

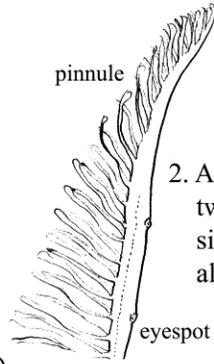
Eyes/Eyespots: Anterior eyespots lacking however, eyespots are present on radiole ribs where each radiole has 5–7 black eyes in a row (Hartman 1969) (Fig. 2) on the dorsal-most radiole pair (Blake and Ruff 2007).

Anterior Appendages: Anterior crown of tentacles made up of two equal parts composed of many radioles (Fig. 1). Radioles, also called cirri or tentacles, are individual branches of the crown and are single and undivided with forked, simple side

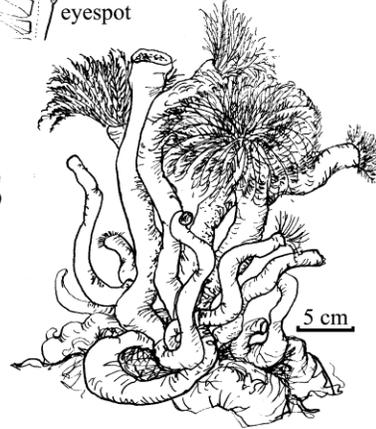
Eudistylia vancouveri



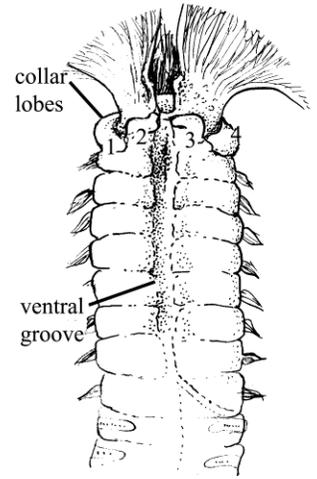
1. *Eudistylia vancouveri*, out of tube x4: a small specimen; thorax of 8 segments; tentacle crown maroon and green striped; many abdominal segments.



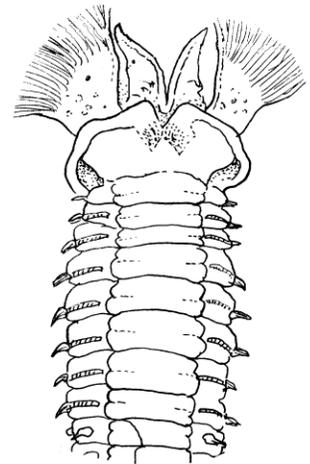
2. A single radiole (cirrus): two rows of side branches simple pinnules; eyespots along rib.



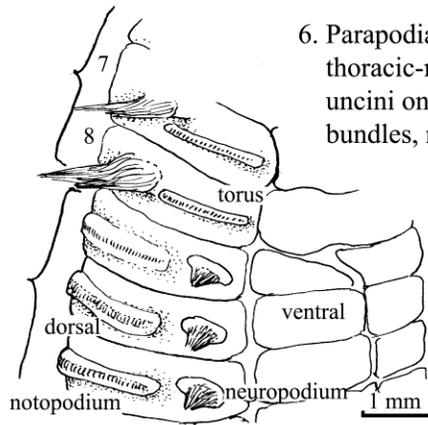
3. Worms, in situ x1/5: dense, shrub-like growth.



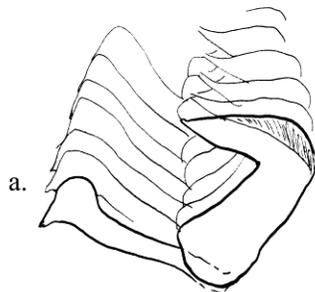
4. Anterior (ventral view): thoracic collar with four lobes.



5. Anterior (dorsal view): dorsal edge of crown without cleft.



6. Parapodia (lateral view) x12: thoracic-neuropodial setae in bundles, notopodial uncini on tori; abdominal- notopodial setae in bundles, neuropodial uncini on tori.



b.

c.

d.

e.

7. Setae:

- a. pennoned setae and avicular uncini (thoracic)
- b. long, bilimbate seta (thoracic)
- c. spatulate seta (thoracic)
- d. pointed seta (abdominal)
- e. avicular uncinus (abdominal)

branches or pinnules (Fig. 2) and dark eyespots along the lower edge, especially near radiole bases (Fig. 2). Bases are spiraled twice (genus *Eudistylia*). Crown conceals mouth and head and edges are smooth and not incised (Hartman 1969) (Fig. 5).

Branchiae: Blood within branchiae is green in color due to the respiratory pigment chlorocruorin (Abbott and Reish 1980; Terwilliger et al. 1975). Branchial base without groove dorsally (Blake and Ruff 2007).

Burrow/Tube: Tube is long, cylindrical, flexible, permanent, tough, leathery and membranous. It is made of mucus and cemented sediment and is not calcareous and without operculum. Worm can completely withdraw into tube.

Pharynx:

Genitalia:

Nephridia:

Possible Misidentifications

Characteristics of the family Sabellidae are the tentacular crown of bipinnate radioles, lack of gills on the body segments and setal types reversed from thoracic to abdominal regions (see **parapodia**). These characters they share with the Serpulidae, however, sabellids are distinct from serpulids by having a leathery tube of mucus and sand which lacks an operculum or trap door. Serpulids, on the other hand, have a calcareous tube and a staked operculum resembling a golf tee (O'Donoghue 1924).

Other tube worms include the Terebellidae, which have soft cirri that cannot be completely retracted into the tube (as sabellids can). Terebellids sometimes have gills on their anterior segments (see *Thelepus crispus* and *Pista pacifica*), and their setal types are not inverted (Blake 1975).

A family with an easily confusing name is the Sabellaridae, which builds sand tubes. These have 2–3 rows of paleae (flattened setae) forming highly modified cephalic structures, but not crowns. Their bodies are clearly defined into thorax, abdomen and long caudal region.

Within the family Sabellidae, there are two subfamilies represented locally, Fabriciinae and Sabellinae. The subfamily

Fabriciinae differs from the Sabellinae in its small size and in its temporary fragile mucus tubes. Several northwest genera exist, including:

Chone species are tiny worms with a membrane partly uniting its radioles and a thoracic collar which is complete and not lobed. Local species have 15 or fewer pairs of radioles.

Fabricia species have few segments and sparse radioles and individuals are quite small. *Amphicorina* has 7–8 abdominal segments, not three.

The subfamily Sabellinae (to which *E. vancouveri* belongs) is noted for its avicular uncini in the thoracic neuropodia, and for its permanent, tough and leathery tubes. Other genera of the sub-family include:

Schizobranhia (=split branch) species are common from central California to Puget Sound (Blake and Ruff 2007). This small worm occurs in great masses on floats. Its radioles are branched, not single and it is often tan colored with a bright red crown (not striped) (Kozloff 1974). *Schizobranhia insignis* (Bush, 1905) often occurs with and is intermixed in clumps with *Eudistylia vancouveri* (Blake and Ruff 2007).

Megalomma species usually occurs in deep water and are rare intertidally. The composite eyes which characterize this genus are spiraled around the radiole ends (Blake 1975).

Pseudopotamilla includes three local species of small, rare tube worms which share with *Eudistylia* the simple pinnate crown of radioles, but the bases of whose two crowns of tentacles are curved into semicircles and are not spiraled.

Sabella species bear two lobes on the thoracic collar, rather than four in *Eudistylia vancouveri*. All members of this genus have spiraled fascicles on their abdominal setae (Knight-Jones and Perkins 1998).

Brispira species are found in membranous tubes on rocky bottoms. This genus was revised in 1998 (Knight-Jones and Perkins) and now includes *Brispira* (= *Sabella*) *crassicornis* which has paired eyespots in deep red bands on its radioles (Blake 1975).

Myxicola species have a thick, transparent mucus sheath or gelatinous tube

covering its body and its radioles are joined by a web for most of their length (Fitzhugh 1989).

Eudistylia vancouveri and *E. polymorpha*, may in fact be the same species (Ricketts and Calvin 1971) and some believe that hybridization occurs (Blake and Ruff 2007). There are two obvious differences between them: *E. polymorpha* does not have striped radioles, they are a solid dark red with orange tips and the dorsal edge of the crown of radioles is not entire (Fig. 5), but is instead notched. *Eudistylia vancouveri* is slightly larger than *E. polymorpha* and the latter is much less likely to be found in large clumps and is the more common species in California (Kozloff 1993). *Eudistylia polymorpha* is also recognizable by a deep cleft or groove, which serves in excretory and gametic transport out of the tube, on each side and at the base of the two spiraled cirri (Blake and Ruff 2007). This groove is ventral and becomes dorsal anteriorly (Kozloff 1993).

Ecological Information

Range: Type locality is Vancouver Island, B.C. (Hartman 1969). NE Pacific range from Alaska to central California.

Local Distribution: In Coos Bay on floating docks or in hummocks. Several hummocks occur just northwest of the OIMB beach.

Habitat: Wharfs, floats, sandy and silty mudflats, as well as vertical rock faces in heavy surf (Kozloff 1974).

Salinity: Found at salinities of >30, in areas of heavy flushing of water. This species doesn't tolerate reduced salinity (Ricketts and Calvin 1971).

Temperature: Cold to temperate.

Tidal Level: Collected on floats just below water surface, intertidal (Hartman 1969).

Associates: Associates include the copepod, *Gastrodelpys dalesi* (at Tomales Point, California), but worm tubes form a complex microhabitat in which many animals and plants survive. Tube hummocks of *Eudistylia vancouveri* are often interspersed with another sabellid, *Schizobranhia insignis* (Blake and Ruff 2007).

Abundance: Gregarious and can be the principal sabellid in rocky habitats (e.g. Puget Sound, Kozloff 1974). Individuals grow in large clumps, in shrub-like masses called

hummocks (Ricketts and Calvin 1971) (Fig. 3).

Life-History Information

Reproduction: Developmental modes among sabellids are highly variable from brooded lecithotrophy, to direct development, and planktonic larvae that are either planktotrophic or lecithotrophic (Crumrine 2001). *Eudistylia vancouveri* are sexual and dioecious although asexual reproduction with some regeneration is also possible. Males, with white sperm, and females, with green eggs, are free spawners and gametes are released through abdominal nephridial pores and into a ventral shallow groove (Fig. 4) and out of tube. Spawning has been observed from late February to July (Washington, Fernald et al. 1987). The development of *Eudistylia vancouveri* is not known.

Larva: There are only two local sabellid species with described larvae and those are *Demonax media* and *Chone infundibuliformis* (Crumrine 2001).

Juvenile:

Longevity:

Growth Rate:

Food: A filter feeder. Plankton particles are trapped by funnel of pinnules and driven by beating cilia, carried down to radiole base where they are sorted and ingested.

Predators: This species is frequently used by humans for fish bait.

Behavior: Individuals can retract fully extended tentacular crown rapidly and does so in response to even slight disturbance, such as a passing shadow. The ability to retract is due to large nerve fibers that allow the worm to withdraw completely into its tube at rates up to 7 m/s (*Eudistylia polymorpha*, Abbot and Reish 1980).

Bibliography

1. ABBOTT, D. P., and D. J. REISH. 1980. Polychaeta: the marine annelid worms, p. 448-489. *In*: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
2. BANSE, K. 1979. Sabellidae (Polychaeta) principally from the northeast Pacific Ocean. *Journal of*

- the Fisheries Research Board of Canada. 36:869-882.
3. BLAKE, J. A. 1975. The Larval development of Polychaeta from the northern California coast. III. eighteen species of Errantia. *Ophelia*. 14:23-84.
 4. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. Carlton (ed.). University of California Press, Berkeley, CA.
 5. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 6. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 7. FITZHUGH, K. 1989. Systematic revision of the Sabellidae-Caobangiidae-Sabellongidae complex (Annelida, Polychaeta). *Bulletin of the American Museum of Natural History*. 192:4-104.
 8. HARTMAN, O. 1969. Atlas of the sedentary polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
 9. JOHNSON, H. P. 1901. The Polychaeta of the Puget Sound region. *Proceedings of the Boston Society of Natural History*. 29:381-437.
 10. KNIGHT-JONES, P., and T. H. PERKINS. 1998. A revision of Sabella, Bispira and Stylomma (Polychaeta : Sabellidae). *Zoological Journal of the Linnean Society*. 123:385-467.
 11. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
 12. KOZLOFF, E.N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA
 13. O'DONOGHUE, C. H. 1924. A note on the polychaetous annelid *Eudistylia gigantea* Bush. *Contributions to Canadian Biology*. 1:443-453.
 14. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 15. TERWILLIGER, R. C., R. L. GARLICK, N. B. TERWILLIGER, and D. P. BLAIR. 1975. Molecular weight of *Eudistylia vancouveri* chlorocruorin and its subunits. *Biochimica et Biophysica Acta*. 400:302-309.

Updated 2014

Magelona sacculata

A burrowing polychaete

Phylum: Annelida
Class: Polychaeta
Order: Canalpalpita, Spionida
Family: Magelonidae

Description

Size: Individuals range in size from 20–30 mm in length and 0.7–1.5 mm in width with approximately 100 segments (Hartman 1961). The illustrated specimen (from Coos Bay) is 30 mm long with 50–80 segments and comprises the following description.

Color: Ivory, with paired dorsal lavender spots (Hartman 1961; Blake 2000). The purple color is due to hemerythrin-containing hemocytes, which are unique to magelonids (Ruppert et al. 2004).

General Morphology: Long, slender and threadlike body bearing extremely long palps anteriorly with a flattened or shovel-like anterior for burrowing (Blake and Ruff 2007).

Body: Body separated into thoracic, consisting of prostomium, peristomium and the first nine setigers, followed by a distinct abdominal region. First segment is a smooth ring and setiger nine is short (Figs. 1, 3). Lateral pouches present between setigers nine and 11 (species *sacculata*) (Blake 2000) (Figs. 1, 3). Body musculature is cross-striated (Ruppert et al. 2004).

Anterior: Prostomium transparent, flattened, shovel-shaped (Fauchald 1977) and often much wider than rest of body. Anterior tip rounded, with slight medial ridge (Fig 2). Prostomium widens posteriorly and has two strong muscles supporting it from below. Prostomium width can be equal to or greater than length (Jones 1963; Blake 2000), but this is not true for our specimens. Peristomium thicker and greater in length than setiger one (Blake 2000).

Trunk: Lateral pouches found between setigers 10–11 (although more commonly 9–10, Blake 2000) and irregularly along abdomen. These are lateral and open anteriorly (Fig. 3) (species *sacculata*, Blake 1975).

Posterior: Pygidium tapers and bears a pair of slender anal cirri (Hartman 1969) (Fig. 1a).

Parapodia: Begin on setiger one (segment two). First eight setigers have biramous parapodia, with pointed setae in both rami (Fig. 6). Thoracic setigers 1–8 biramous with noto- and neuropodia foliaceous and elevated. Thoracic notopodia bear dorsal medial lobe with lateral lamellae while neuropodia have a ventral lobe (Blake 2000). Setiger nine with specialized setae (unlike those of setigers 1–8) and conspicuous lateral lamellae. Abdominal parapodia have small dorsal and ventral medial lobes and broad, lateral lamellae where notch is produced as noto- and neuropodial lamellae almost overlap (Fig. 5).

Setae (chaetae): Several types of setae are observed: (1) limbate (simple, capillary, with flattened margin which can be pennoned and is found in both rami in setigers 1–9 and abdominal notopodia (Fig. 6), (2) crenulate setae (clubbed, like a molar), found as specialized setae on setiger nine (Jones 1963) (Figs. 4, 7), (3) mucronate (sharp tip and abruptly tapered) found as specialized setae, also on setiger nine (but not on these specimens, Fig. 8) and (4) hooded hooks (each with a large fang and two small teeth), of uniform size (species *sacculata*, Hartman and Reish 1950) found only abdominally (Blake 2000) (Fig. 9).

Eyes/Eyespots: None.

Anterior Appendages: No horns or appendages, but with a ventral pair of conspicuous, elongate papillate palps (family Magelonidae). Palps are long (extending to setiger 26), adhesive and coarsely papillated (Hartman 1961; Blake 2000). They are attached ventrally at the junction of peri- and prostomiums (Fauchald 1977).

Branchiae: None.

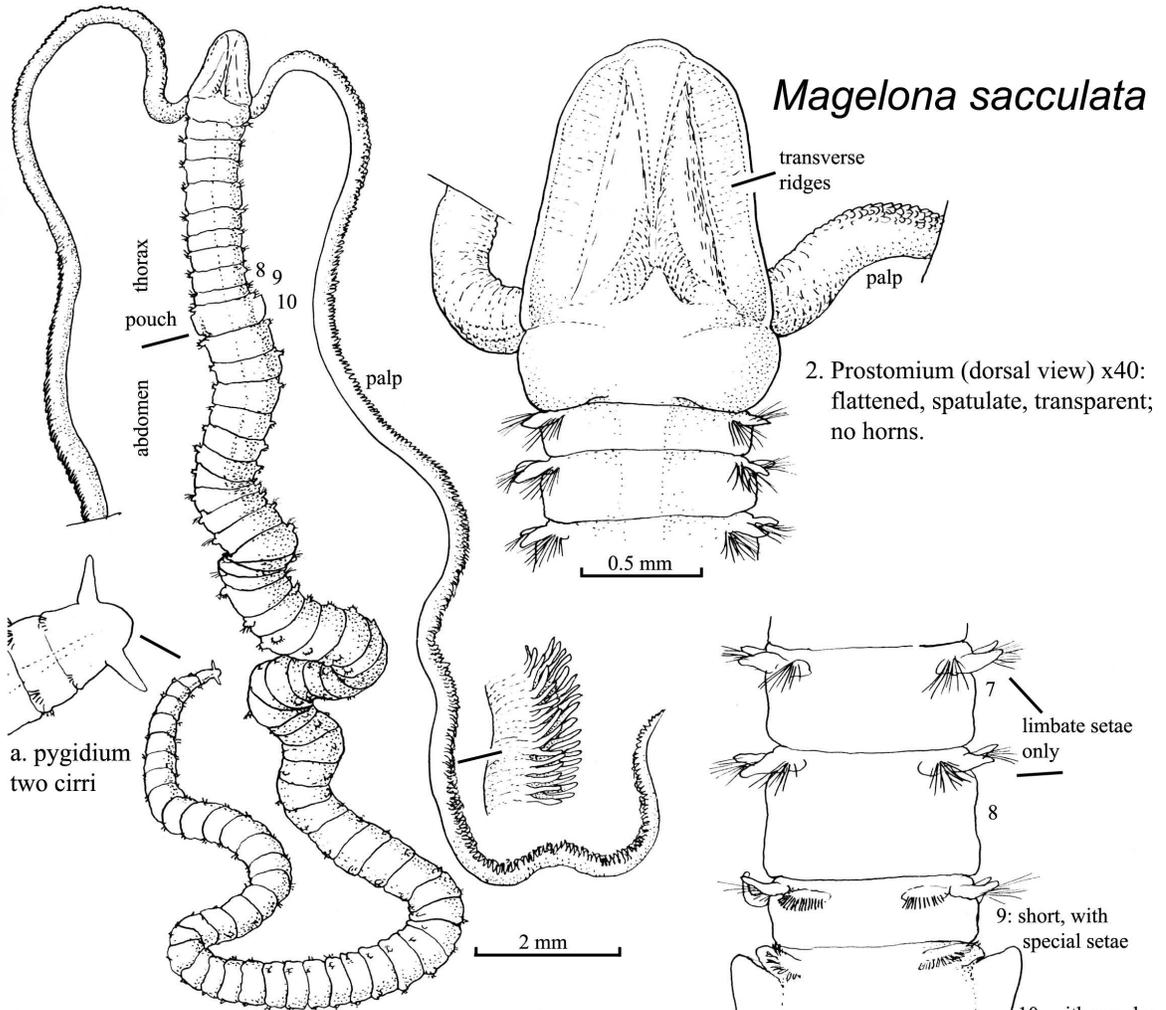
Burrow/Tube: Magelonids are good burrowers (see **Behavior**), but do not inhabit a permanent tube or burrow.

Pharynx: Bears proboscis which is smooth and globular when everted (Hartman 1961).

Genitalia:

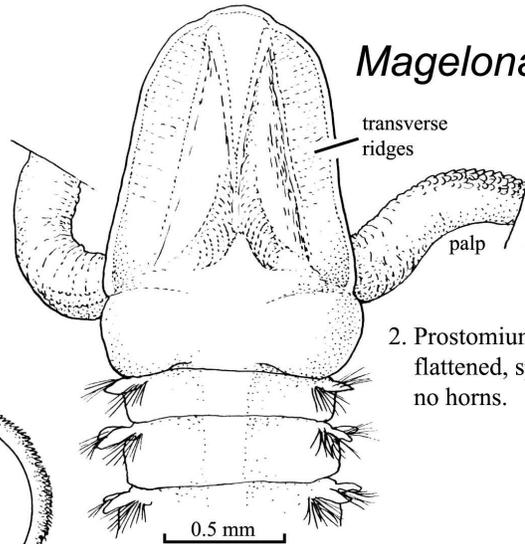
Nephridia:

Magelona sacculata

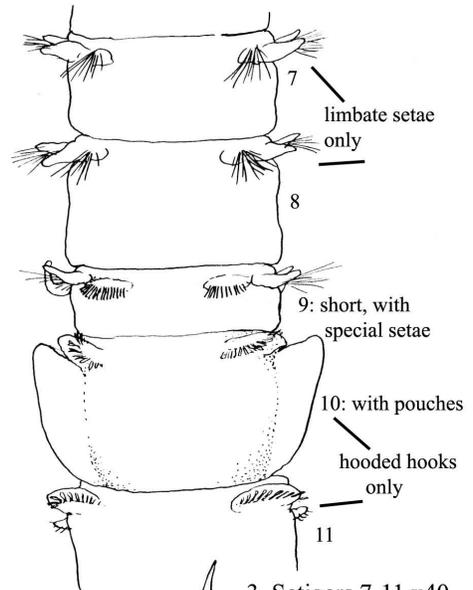


a. pygidium
two cirri

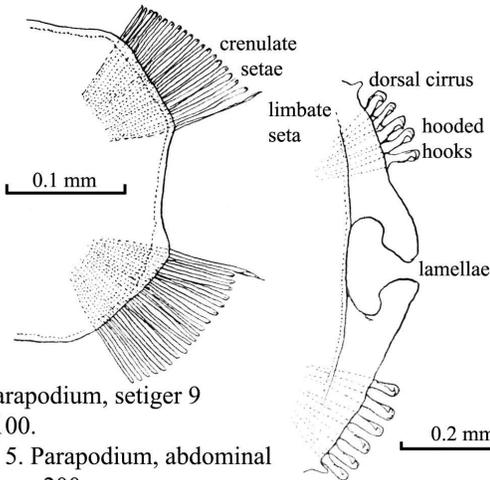
1. *Magelona sacculata* (L:30mm) x12: obvious thorax and abdomen, long palps; no branchiae or genital spines; lateral pouches between setigers 10 and 11; setiger 9 short.



2. Prostomium (dorsal view) x40: flattened, spatulate, transparent; no horns.



3. Setigers 7-11 x40.



4. Parapodium, setiger 9 x100.

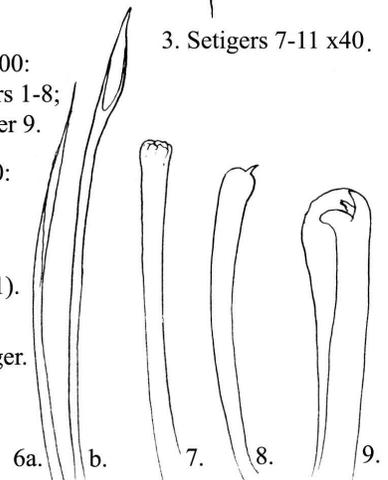
5. Parapodium, abdominal x200.

6. Limbate setae x300:
a. capillary, setigers 1-8;
b. pennoned, setiger 9.

7. Crenulate seta x600:
from setiger 9.

8. Mucronate seta
(from Hartman 1961).

9. Hooded hook x600:
from abdominal setiger.



Possible Misidentifications

There are three other large, common families of the order Spionida. The Spionidae, a very numerous and diverse group is characterized by grooved palps. Unlike Magelonidae, they have palps which are not papillate, adhesive, or exceedingly long. Their prostomiums are not flattened and they often have eyes, nuchal tentacles and/or branchiae, where magelonids do not. Cirratulidae have long palps and long, filamentous gills, which are lacking in the Magelonidae. The Chaetopteridae, also a Spionida family, have very distinct body regions, thick spines on setiger four, and often have fan-like medial parapodia. Their tubes are parchment-like or annulated (Fauchald 1977).

Trochochaetidae and Longosomatidae (= Heterospionidae) are small, obscure spionid families each containing only one genus. Trochochaetidae have bodies divided into two regions, a large flattened prostomium with a pair of palps, a single occipital tentacle and two pairs of parapodia directed forward. Like the Magelonidae, they are not tube dwellers.

Longosomatidae have short thoracic and very long abdominal setigers. They have a prostomium without appendages and a pair of palps as well as filiform branchiae on the thorax. They do not inhabit the intertidal zone. Poecilochaetidae are spionids with long, slender bodies. They have a small prostomium with a single antenna and palps and their parapodia have prominent dorsal and ventral cirri.

Magelona is one of three genera in the family Magelonidae where there are 70 described species (Clark et al. 2010). Members of the genus *Meredithia* (Hernández-Alcántara & Solis-Weiss, 2000) possess large hooded and curved spines in some abdominal setigers (Clark et al. 2010). The genus *Ocomagelona* (Aquirrezabalaga et al. 2001) is characterized by eight thoracic setigers (instead of nine) (Clark et al. 2010).

The characters which are used to differentiate members of the genus *Magelona* include the prostomium morphology (size and presence or absence of frontal horns), presence or absence of medial lobes on thoracic notopodia, position or presence of lateral pouches, modified

setal morphology on setiger nine, morphology of abdominal hooded hooks, abdominal medial lamellae and the presence or absence and morphology of inter lamellae on abdominal parapodia (Blake and Ruff 2007). *Magelona sacculata* is unique in having large, lateral open pouches between setigers 10 and 11, uniform hooded hooks on the abdominal parapodia and mucronate or crenulate specialized setae on setiger nine.

Other species in the genus include: *Magelona pacifica* (Monro, 1933), seemingly a southern species, is unlikely to be found in Oregon (Hartman 1969). *Magelona cerae* (Hartman 1950; Hartman and Reish 1950) was found at depths of 37-73 m off Coos Bay forming beds in sand, but further reports of this species are lacking. Individuals are up to 10 mm in length, the prostomium has slight, blunt horns at the corners. The thoracic notopodia have a dorsal cirrus which disappears by the ninth segment. Each of the abdominal hooded hooks has one large fang with a small tooth above it. *Magelona californica* (Hartman, 1944), although found in southern California, is considered a northeastern Pacific species by Hartman (1969). It has a rounded prostomium like that of *M. sacculata*, but it lacks lateral pouches and its abdomen is abruptly wider than the thorax (Hartman 1969). *Magelona pitelkai* (Hartman, 1944), has been reported from Coos Bay as well as Washington and British Columbia, but its identity has not been confirmed (Jones 1978). This is a large species with 54 segments reaching 35 mm in length. The prostomium has a truncate margin and the special setae on setiger nine have pennoned tips, not mucronate ones. *Magelona pitelkai* lacks lateral pouches and is the most common magelonid in central and northern California (Blake 1975). *Magelona pitelkai* can be distinguished from *M. sacculata* in that the former species has small, deeply embedded and modified hooks in addition to the larger hooks. *Magelona sacculata*, on the other hand has only one hook type (Blake 2000). *Magelona longicornis* (Johnson, 1901), (= *M. japonica* Okuda, 1937 (Jones 1971)) has prostomial horns, lateral parapodial lamellae in setigers 1–8, no modification on the ninth parapodium, bidentate hooded hooks

(Jones 1971) and no lateral pouches. This species is the one most likely to be found in Puget Sound (Kozloff 1974). *Magelona berkeleyi* (Jones, 1971) has inconspicuous anterior prostomial horns, extended lateral lamellae on its parapodia and no lateral pouches. Like *M. sacculata*, it has tridentate hooded hooks, but it has no specialized setae on the ninth setiger (Blake 2000). *Magelona berkeleyi* is reported from central California to Washington (Blake 2000).

Ecological Information

Range: Type locality is San Pedro Shelf, California (Hartman 1969). NE Pacific distribution ranges from British Columbia (Hobson and Banse 1981) to southern California (Hartman 1969).

Local Distribution: Oregon distribution, Yaquina Bay and Umpqua estuaries. Coos Bay sites include the inner bay and South Slough.

Habitat: Fine sands, silt (Blake 1975) and sandy mud in Coos Bay (South Slough). Builds poorly supported burrows with no distinct or permanent tube.

Salinity: Found at salinities of 30 in Coos Bay.

Temperature:

Tidal Level: More likely to be found subtidally than intertidally in Oregon. Occurs subtidal to 50 m in southern California (Hartman 1969; Blake 2000).

Associates:

Abundance: Considered rare from central California to Oregon, where *M. pitelkai* is more common (Blake and Ruff 2007). However, in Oregon it may be the most common magelonid.

Life-History Information

Reproduction: The development of *M. sacculata* is not known. Wilson (1982) described the development of three magelonid species from the southern coast of England including *Magelona alleni*, *M. filiformis* and *M. mirabilis*. Among these three species, which reproduce by broadcast spawning, oocyte diameters ranged from 100–150 µm in diameter with natural spawning speculated in late summer (August), near Plymouth, England (Wilson 1982; Blake 2006).

Larva: Magelonid larvae are pelagic. They are recognizable by long anterior larval tentacles that coil (Wilson 1982; Crumrine 2001; Pernet et al. 2002), reaching lengths of or exceeding the larval body length.

Magelonid larvae also have two bunches of long setae (four in each bunch, Wilson 1982) that arise from chetal sacs just below the larval tentacles. The three *Magelona* species with described development (Wilson 1982) developed into trochophore larvae after about a day. In these species, Wilson (1982) noted the elongation of the prototrochal region (= tentacles) and two eyes once larvae were three days old. An unidentified megalonid larva is commonly seen in plankton samples in Coos Bay which may be the larva of *M. cercae* (Crumrine 2001) or *M. sacculata*. (<http://invert-embryo.blogspot.com/2010/05/nechtochaete-larva-of-polychaete.html>)

Juvenile:

Longevity:

Growth Rate:

Food: A motile surface deposit feeder which chooses large particles of detritus and diatoms. Small crustaceans are captured on papillated surface of palps. A looping motion moves food up the palp and mucus may help final movement into mouth. Some suspension feeding may also take place. Magelonid larvae feed on veligers (Fauchald and Jumars 1979, Johnson and Brink 1998).

Predators:

Behavior: *Megalona sacculata* is a good burrower which is aided by its shovel-like head.

Bibliography

1. BLAKE, J. A. 2000. Family Mageloidae Cunningham and Ramage, 1888, p. 253-261. *In:* Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
2. —. 2006. Spionida, p. 565-638. *In:* Reproductive biology and phylogeny of annelida. G. Rouse and R. Pleijel (eds.). Science Publishers, Enfield, New Hampshire.

3. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
4. CLARKE, D. T., G. L. J. PATERSON, W. K. FLORENCE, and M. J. GIBBONS. 2010. A new species of *Magelona* (Polychaeta: Magelonidae) from southern Namibia. *African Natural History*. 6:77-82.
5. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
6. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County Science Series*. 28:1-190.
7. FAUCHALD, K., and P. A. JUMARS. 1979. Diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology*. 17:193-284.
8. HARTMAN, O. 1961. Polychaetous annelids from California. University of Southern California Press, Los Angeles, CA.
9. —. 1969. Atlas of the sedentariate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
10. HARTMAN, O., and D. J. REISH. 1950. The Marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
11. HOBSON, K. D., and K. BANSE. 1981. Sedentariate and archiannelid polychaetes of British Columbia and Washington. *Canadian Bulletin of Fisheries and Aquatic Sciences*. 209:1-144.
12. JOHNSON, K. B., and L. A. BRINK. 1998. Predation on bivalve veligers by polychaete larvae. *Biological Bulletin*. 194:297-303.
13. JONES, M. L. 1963. Four new species of *Magelona* (Annelida, Polychaeta) and a redescription of *Magelona longicornis* Johnson. American Museum of Natural History, New York, N.Y.
14. —. 1971. *Magelona berkeleyi* n.sp. from Puget Sound (Annelida: Polychaeta), with a further redescription of *Magelona longicornis* Johnson and a consideration of recently described species of *Magelona*. *Journal of the Fisheries Research Board of Canada*. 28:1445-1454.
15. —. 1978. Three new species of *Magelona* (Annelida, Polychaeta) and a description of *Magelona pitelkai*. *Proceedings of the Biological Society of Washington*. 91:336-363.
16. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
17. PERNET, B., P. Y. QIAN, G. ROUSE, C. M. YOUNG, and K. J. ECKELBARGER. 2002. Phylum Annelida: Polychaeta. *In*: Atlas of marine invertebrate larvae. C. M. Young, M. A. Sewell, and M. E. Rice (eds.). Academic Press, San Diego, CA.
18. RUPPERT, E.E., R.S. FOX, and R.D. BARNES. 2004. Invertebrate zoology: a functional evolutionary approach, 7th Edition. Thomson Brooks/Cole, Belmont, CA.
19. WILSON, D. P. 1982. The Larval development of three species of *Magelona* (Polychaeta) from localities near Plymouth. *Journal of the Marine Biological Association of the United Kingdom*. 62:385-401.

Updated 2014

Boccardia proboscidea

A burrowing spionid worm

Phylum: Annelida
Class: Polychaeta
Order: Canalpalpita, Spionida
Family: Spionidae

Taxonomy: *Boccardia proboscidea*'s senior subjective synonym, *Polydora californica* (Treadwell, 1914) and an un-typified name, *Spio californica* (Fewkes, 1889) were both suppressed in 2012 by the International Commission on Zoological Nomenclature (ICZN, case 3520). The widely cited and used name, *Boccardia proboscidea* (Hartman, 1940) was conserved (ICZN 2012).

Description

Size: Specimens up to 30–35 mm in length and 1.5 mm in width, where length extends with age (Hartman 1940). The illustrated specimen has approximately 130 segments (Fig. 1).

Color: Yellow-orange with red branchiae and dusky areas around prostomium and parapodia (Hartman 1969). Sato-Okoshi and Okoshi (1997) report black pigment following the prostomial ridge and palpal grooves.

General Morphology: Spionid polychaete with thick anterior palps, conspicuous segmentation.

Body: Long, depressed, somewhat flattened body that tapers posteriorly (Hartman 1940). First setiger small capillary setae in bunches (Fig. 5a). Setiger five is modified with two kinds of dark, strong setae in notopodia. Setiger five is almost twice the length of setiger four (Figs. 2, 3) (Hartman 1940).

Anterior: Prostomium long, rounded, without medial groove and snout-like (species *proboscidea*, Hartman 1940). Caruncle (sensory organ) present and extends to setiger three (Fig. 3) (Hartman 1969).

Trunk:

Posterior: Pygidium is a round, flaring disc with four unequal lobes where dorsal lobes are smaller (Fig. 4) (Hartman 1969).

Parapodia: Biramous after first setiger. Podia on the first setiger are not lobed, small and inconspicuous. The second setiger's parapodial lobes become twice as large as the first's, and continue to worm posterior.

Setae (chaetae): All setae are simple and include bunches of short, capillary spines to setiger six (except for modified setiger five) (Figs. 5a, b). A transverse row of approximately eight neuropodial uncini (hooded hooks) with bifid (two-pronged) tips begins on setiger seven and continues to posterior end (Fig. 5e), with bunches of capillary setae below them (until setiger 11). Notosetae of setiger five are heavy, dark and arranged vertically in two rows of five with pairs of long, falcate spines (Fig. 5c) and shorter brush-topped clubs (Fig. 5d) while the neurosetae are capillary (Hartman 1969). All notosetae are capillary except for those of setiger five.

Eyes/Eyespots: Up to six (4–6) eyespots between palpal bases (Fig. 3).

Anterior Appendages: Long, simple, longitudinally grooved tentacle-like palps (family Spionidae) (Fig. 1).

Branchiae: The gill-like structures in this species are long, single vascular processes that are present on setigers 2–4, and from setiger seven to (almost) the worm posterior end (Figs. 2, 3).

Burrow/Tube: Individuals build vertical, U-shaped burrows in rocky shale or amongst and within bivalve shells (Bailey-Brock 2000).

Pharynx:

Genitalia:

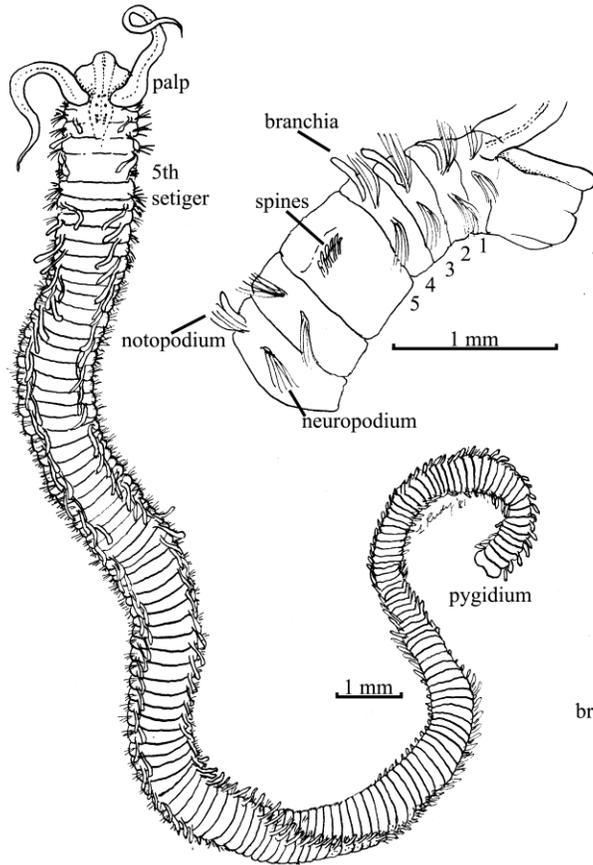
Nephridia:

Possible Misidentifications

Spionid polychaetes are distinguished by their long palps. Two other polychaete families have long palps: the Magelonidae, with adhesive palps (not long and flowing) and with flattened spade-like prostomiums and the Chaetopteridae which have palps, but their bodies are very obviously divided into three quite different regions.

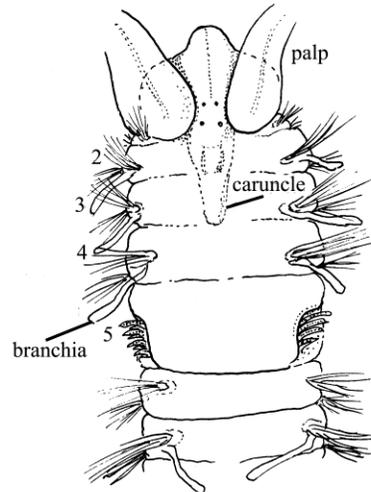
The genus *Boccardia* contains 22 species (Simon et al. 2010) and members of this genus and the genus *Boccardiella* have branchiae on setigers anterior to setiger

Boccardia proboscidea

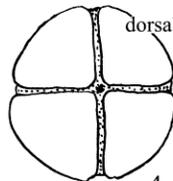


1. *Boccardia proboscidea* x12:
typical spionid palps; body flattened,
depressed; pygidium a flaring disk.

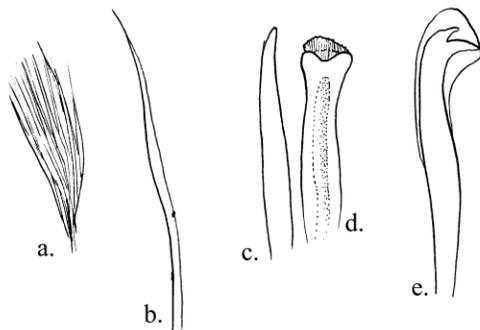
2. Anterior (lateral view) x30:
biramous parapodia with branchiae;
fifth setiger wide, modified, with stout
dorsal spines.



3. Anterior (dorsal view) x30:
prostomium rounded, snout-like; 4-6 eyes;
inconspicuous parapodia on first setiger;
setiger 5 with dorsal spines; caruncle
obvious.



4. Pygidium (posterior view) x40:
dorsal lobes smaller.



5. Setae:
a. neuropodial fascicle.
b. capillary from a.
c. falciger from setiger 5.
d. brush-topped club, setiger 5.
e. neuropodial hooded hook.

five. These two local genera differ in the kinds of modified setae on the fifth setiger, *Boccardiella* species have one (simple and falcate) while *Boccardia* have two (one simple and falcate and the second expanded and club-like) (Blake and Ruff 2007).

Boccardiella hamata (= *Boccardia uncata*) has recurved spines, rather than straight bifid uncini, on its posterior parapodia and the pygidium has two lappets (Hartman 1969). It is common in oyster beds and builds tubes in mudflats or bores holes into hermit crab and bivalve shells and is reported from central California to Oregon (Blake and Ruff 2007) and in Vancouver Island, Canada (Sato-Okoshi and Okoshi 1997). *Boccardiella truncata* is green in color, has a saucer-like pygidium and a truncate anterior end. It is not usually estuarine and is, instead, more common intertidally in sandstone cliffs in northern California (Blake and Ruff 2007).

Two species of *Boccardia* have both falcate and brush-topped setae on setiger five as seen in *B. proboscidea*. *Boccardia berkeleyorum* is reported from central California and has no notosetae on setiger one, only neurosetae (Blake and Ruff 2007). Its bristle-topped setae (on setiger five) have a small accessory tooth at the distal end and the posterior notopodia have acicular setae (Blake 1975). This species bores in coralline algae, hermit crab shells and the jingle shell *Pododesmus* sp. *Boccardia columbiana* resembles *B. proboscidea* most closely. Its chief difference is that the fascicles of fine setae on setiger one are long and fanned forward, where they are short on *B. proboscidea*. This species is reddish-brown, and bores into wood pilings and coarse algae. *Boccardia proboscidea* was the only member of this genus found in Oregon by Hartman and Reish (Hartman and Reish 1950).

Boccardia polybranchia and *B. tricuspa* have two kinds of setae on setiger five. *Boccardia polybranchia* is green to reddish-yellow in color and has a notched prostomium. Its first setiger lacks notosetae, it has only 60–80 segments and a pygidium that is a thick ring. *Boccardia polybranchia* is a cosmopolitan species that

lives in estuarine mud and is reported in western Canada (Hartman 1969) but not between central California and Oregon (Blake and Ruff 2007). *Boccardia tricuspa* has two kinds of setae on setiger five, which are falcate and tridentate (not bruso-topped). Its branchiae are anterior to setiger five and are small and inconspicuous. It bores in molluscs and is usually a more southern species than *B. proboscidea*.

Ecological Information

Range: Type locality is Caspar, California. NE Pacific range, western Canada south to southern California (Hartman 1969).

Local Distribution: Coos Bay distribution includes the outer rocky coast and offshore (Hartman and Reish 1950).

Habitat: Burrows are found amongst *Mytilus* spp. (mussel) colonies and individuals inhabit a variety of niches (Hartman 1940).

Salinity: Collected at 30 and exhibits a great toleration for salinity variation (Hartman 1940).

Temperature: *Boccardia proboscidea* residence in tidepools is evidence of a wide temperature tolerance (Hartman 1940).

Tidal Level: High rocky intertidal pools and in high intertidal crevices (Blake 1975).

Associates: *Mytilus* spp. and its accompanying organisms in rocky crevices. An additional associate is the small, red harpacticoid copepod, *Tigriopus* sp. (Hartman 1940).

Abundance: The only *Boccardia* species found in Oregon by Hartman and Reish, (1950) where it is the most common member of a common family (Hartman 1940).

Life-History Information

Reproduction: Eggs, in five or more capsules of 50 eggs each, are deposited in a tube and aerated during development by adult's rhythmic movement (Hartman 1940). Egg capsules are present from August to October in Barkley Sound, Canada (Sato-Okoshi and Okoshi 1997). Embryonic development is rapid and easily occurs in the lab where capsules in the same tube often exhibit different development modes. For this reason, the larval development of *B. proboscidea* is a model for poecilogony (differing developmental strategies within the

same species, Gibson et al. 1999) among spionids (Blake and Ruff 2007). Woodwick (1977) reported two egg sizes, 100 and 150 µm, which emerge as planktotrophic (emerging at 3-setiger stage) and lecithotrophic (emerging at up to 15-setiger stage) larvae, respectively. Later, Blake and Kudenov (1981) observed nurse eggs within capsules which are ingested by and support larvae within the capsule, coupled with adelphophagy (consumption of one embryo by another) on smaller larvae. These developmental strategies were summarized by Oyarzun et al. (2011) and consists of females which produce capsules with 1) planktotrophic larvae, 2) planktotrophic larvae and nurse eggs and 3) planktotrophic larvae, nurse eggs and adelphophages larvae. The variation in capsule composition depends on female behavior and latitude, where individuals at higher latitudes produce more adelphophages larvae which emerge at advanced stages and settle quickly (Oyarzun et al. 2011).

Larva: Larval stages found in plankton in the summer (Hartman and Reish 1950) and larval development is described (Blake and Kudenov 1981; Gibson and Smith 2004). Larvae develop through trochophore and metatrochophore stages and have a single dorsal chromatophore in young stages and two beginning at the 5-setiger stage (Blake and Kudenov 1981). Larvae also possess three pairs of black eyes. Once larvae reach the nectochaete stage, they can be identified by adult characters (e.g. modified setae on setiger five, branchiae beginning on setiger) (Crumrine 2001).

Juvenile: Metamorphosis is gradual and occurs between the 13–15 setiger stages where larval structures are lost and juvenile features are gained. Juvenile features include setal morphology like that of the adults where the length and number increase with growth. Branchiae develop first on setigers 7–9 and appear later in anterior and posterior setigers. The juvenile pygidium is like that of the adult, comprising four lobes (Gibson and Smith 2004).

Longevity:

Growth Rate:

Food: Spionids feed by sweeping their tentacles across the surface of substrate where particles are collected and wiped on

the underside of prostomium (Dales 1967). *Boccardia proboscidea* eats small copepods (Hartman 1940) and is a voracious predator on algal particles, Bryozoa, Hydrozoa, other attached and free-swimming animals (Hartman 1940).

Predators:

Behavior: A colonial burrower, *B. proboscidea* can be seen with tentacles protruding from burrow (Ricketts and Calvin 1971).

Bibliography

1. BAILEY-BROCK, J. H. 2000. A new record of the polychaete *Boccardia proboscidea* (family Spionidae), imported to Hawai'i with oysters. *Pacific Science*. 54:27-30.
2. BLAKE, J. A. 1975. Phylum Annelida: Class Polychaeta, p. 151-243. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
3. BLAKE, J. A., and J. D. KUDENOV. 1981. Larval development, larval nutrition and growth for two *Boccardia* species (Polychaeta: Spionidae) from Victoria, Australia. *Marine Ecology Progress Series*. 6:175-182.
4. BLAKE, J. A., and R. E. RUFF. 2007. Polychaeta, p. 309-410. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
5. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In: Identification guide to karval narine unvertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
6. DALES, R. P. 1967. *Annelids*. Hutchinson & Co., Ltd., London.
7. GIBSON, G., I. G. PATERSON, H. TAYLOR, and B. WOOLRIDGE. 1999. Molecular and morphological evidence of a single species, *Boccardia proboscidea* (Polychaeta : Spionidae), with multiple development modes. *Marine Biology*. 134:743-751.
8. GIBSON, G. D., and H. L. SMITH. 2004. From embryos to juveniles:

- morphogenesis in the spionid *Boccardia proboscidea* (Polychaeta). *Invertebrate Biology*. 123:136-145.
9. HARTMAN, O. 1940. *Boccardia proboscidea*, a new species of spionid worm from California. *Journal of the Washington Academy of Science*. 30:382-397.
 10. —. 1969. Atlas of the sedentariate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
 11. HARTMAN, O., and D. J. REISH. 1950. The Marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
 12. INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 2012. Opinion 2303. (Case 3520) *Boccardia proboscidea* Hartman, 1940 (Annelida, Spionidae): specific name conserved. *Bulletin of Zoological Nomenclature*. 69:232-234.
 13. OYARZUN, F. X., A. R. MAHON, B. J. SWALLA, and K. M. HALANYCH. 2011. Phylogeography and reproductive variation of the poecilognous polychaete *Boccardia proboscidea* (Annelida: Spionidae) along the West Coast of North America. *Evolution & Development*. 13:489-503.
 14. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 15. SATO-OKOSHI, W., and K. OKOSHI. 1997. Survey of the genera *Polydora*, *Boccardiella* and *Boccardia* (Polychaeta, Spionidae) in Barkley Sound (Vancouver Island, Canada), with special reference to boring activity. *Bulletin of Marine Science*. 60:482-493.
 16. SIMON, C. A., T. M. WORSFOLD, L. LANGE, and J. STERLEY. 2010. The genus *Boccardia* (Polychaeta: Spionidae) associated with mollusc shells on the south coast of South Africa. *Journal of the Marine Biological Association of the United Kingdom*. 90:585-598.
 17. WOODWICK, K. H. 1977. Lecithotrophic larval development in *Boccardia proboscidea* Hartman, p. 347-371. *In: Essays on polychaetous annelids in memory of Dr. Olga Hartman*. D. J. Reish and K. Fauchald (eds.). Allan Hancock Foundation, University of Southern California, Los Angeles, California.

Updated 2014

Polydora nuchalis

A spionid worm

Phylum: Annelida
Class: Polychaeta
Order: Canalpalpita, Spionida
Family: Spionidae

Taxonomy: *Polydora* was revised in 1996 by Blake who noted two distinct categories within the genus which were consistently recognizable with both adult and larval phenotypes. These two categories led to the two genera, *Polydora* and *Dipolydora* (Blake 1996).

Description

Size: Specimens up to 28 mm in length.

Color: The illustrated specimen (Fig. 2) is pale orange, with a broad red vertical dorsal stripe, red cirri and palps.

General Morphology: A small, thin and delicate spionid worm.

Body: Body morphology is easily recognizable as *Polydora* because of a modified fifth setiger (Fig. 4).

Anterior: Prostomium blunt, trilobed and with obvious nuchal (olfactory) tentacle dorsally (Fig. 1). Caruncle extends to third segment (Woodwick 1953) (Fig. 1).

Trunk: Main body consists of eighty segments or more.

Posterior: Pygidium lacks papillae (Fig. 2).

Parapodia: Biramous.

Setae (chaetae): The first setiger has several short and winged neurosetae, but no notosetae. Setigers 2–4 have capillary setae (Bailey-Brock 1990). Setiger five is modified with special setae, no post-setal lobe and, instead, bears a crescent shaped row of spines (Fig. 4). Two types of spines are present on setiger five: one simple and falcate (Fig. 3a) and the other plumose (Fig. 3b). Hooded hooks on neuropodia begin on setiger seven.

Eyes/Eyespots: Two eyespots situated anteriorly, at the base of each palp (Fig. 1) (Bailey-Brock 1990).

Anterior Appendages: Tentacular palps are long and coiling and extend to 25 segments (Fig. 2).

Branchiae: Strap-like branchiae begin on setiger seven (Fig. 4).

Burrow/Tube: Orange tubes are approximately 2 cm in length.

Pharynx:

Genitalia:

Nephridia:

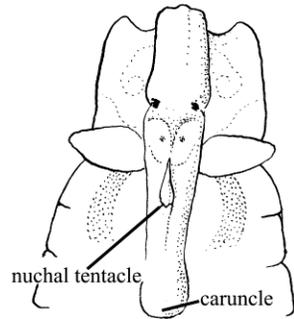
Possible Misidentifications

Spionidae can be distinguished by a pair of long prehensile grooved palps which arise from the posterior peristomium (Blake 1996). Two other polychaete families have long palps: the Magelonidae, with adhesive palps (not long and flowing) and with flattened spade-like prostomiums and the Chaetopteridae which have palps, but their bodies are very obviously divided into three quite different regions, which is not the case in spionids. The similar family Cirratulidae may also have a large pair of palps, but they have tentacular filaments, which are lacking in the spionids. Spionids also have hooded hooks in posterior segments, may or may not have prostomial appendages or branchiae, the prostomium is well developed and fused with peristomium, the pharynx is without jaws and the setae are mostly simple (Blake 1975). Often certain segments are highly modified and have special setae, for example prostomial horns are present in some genera. Spionid parapodia are biramous, with acicula (see *Leitoscoloplos pugettensis*) and sometimes have stout saber setae. There are 19 local spionid genera (Blake and Ruff 2007).

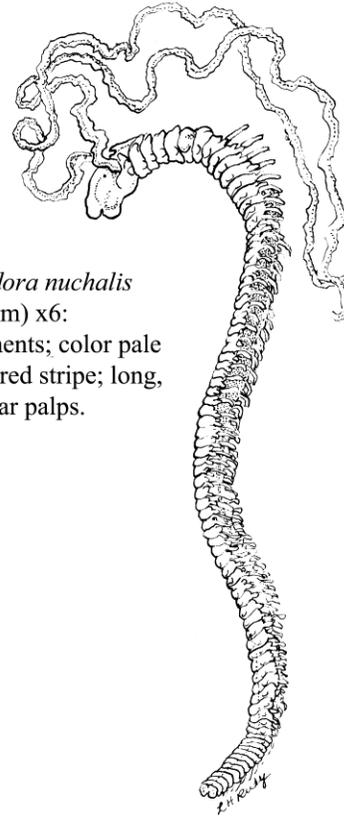
Superficially similar species in the genus recently separated from *Polydora*, *Diplopolydora*, are *D. elegantissima* and *D. socialis* (Blake and Ruff 2007).

Diplopolydora elegantissima, a boring species, has very short branchiae beginning on the eighth setiger, but rarely on the

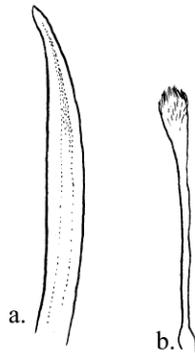
Polydora nuchalis



1. Prostomium (dorsal view).

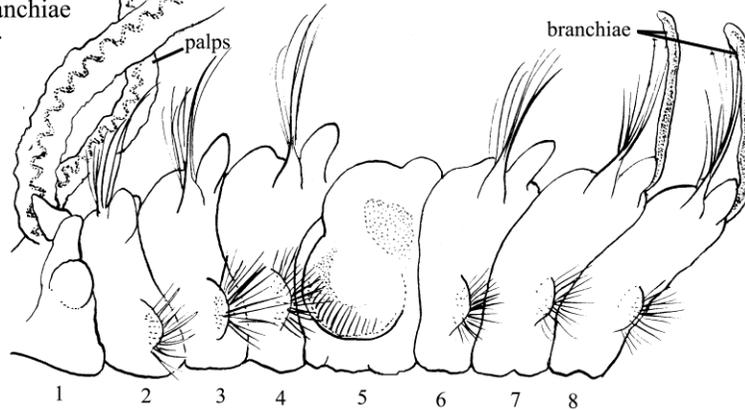


2. *Polydora nuchalis*
(L: 28mm) x6:
80 segments; color pale
orange, red stripe; long,
tentacular palps.



3. Spines of setiger five:
a. heavy spines; simple, falcate
(sickle-like).
b. companion setae, fine, plumose.

4. First eight setigers (lateral view):
showing modified fifth setiger with
crescentic row of spines, no post
setal lobe; strap-like branchiae
(gills) beginning setiger
seven.



seventh, and its nuchal caruncle extends back over several segments. *Diplopolydora socialis*, common in San Francisco, California also has branchiae beginning on the eighth setiger. *Diplopolydora* species are recognizable from *Polydora* species by the following characteristics: hooded hooks having curved shafts and no constriction or manubrium, the main fang is directed apically, notosetae are present on setiger one and the anterior digestive tract is enlarged (Blake 1996).

The genus *Polydora* contains ten locally occurring species (see Blake 1996 for dichotomous key), most are known only to California, but many likely occur in Oregon as well. *Polydora allopuris* is a subtidal species and bores into the shells of *Stylaster californicus*. It has a rounded prostomium, no occipital antennae and two eyes. *Polydora pygidialis* and *P. websteri* bore into mollusk shells, ectoprocts and other calcareous substrates, the former species with a rounded prostomium and up to four eyes, while the latter has an incised prostomium and four eyes. *Polydora bioccipitalis* occurs in southern California and Chile in intertidal and shallow subtidal zones and has a prostomium with a deep anterior notch, two occipital antennae and four eyes. *Polydora brevipalpa* can be found among bivalve and gastropod shells and *P. limicola* can be found in large groups and attached to rocks, wharves and ships. *Polydora brevipalpa* has a rounded prostomium and palps with black bands. *Polydora limicola* has a weakly incised prostomium and four eyes and black pigment bands, anteriorly and dorsally. *Polydora narica* occurs subtidally off Monterey, California and has a large and blunt prostomium and inflated caruncle. *Polydora spongicola* is a commensal species living with sponges that possesses a weakly rounded prostomium and four eyes (Blake 1996).

Polydora cornuta (= *P. ligni*), the type species for this genus is also the most similar species to *P. nuchalis*. *Polydora cornuta* has a nuchal tentacle and its branchiae also begin on setiger seven. Its heavy spines on setiger five have an accessory tooth and its companion setae are feather-like. This species has four eyes anteriorly, arranged in a square and, posteriorly, a large cup-like pygidium with

dorsal notch. Differing from *P. nuchalis*, *P. cornuta* has a bilobed prostomium, rather than incised. *Polydora cornuta* is found in mud or water-logged wood and it is also an oyster borer (Blake and Evans 1973).

Ecological Information

Range: Type locality is southern California (Blake 1996) and the distribution ranges from Oregon to California.

Local Distribution: Coos Bay distribution includes South Slough.

Habitat: Mudflats of estuaries and bays (Blake 1975) or bottom of a drainage channel, *Salicornia* sp. marshes and on non-calcareous substrates (Blake and Evans 1973).

Salinity: Collected at salinities of 10 in surface waters of Coos Bay.

Temperature: Collected at temperatures ranging from 8–18°C in surface waters of Coos Bay.

Tidal Level: Collected at +1.4 m in South Slough.

Associates: Associates include amphipods, isopods, the gastropod *Ovatella* sp. and the alga *Fucus* sp.

Abundance:

Life-History Information

Reproduction: Fertilization is internal and females release pinkish eggs (120 µm in diameter) into transparent capsules through nephridial canals (Woodwick 1960). Up to 100 eggs are kept in the capsules in chains or attached to adult tube walls. Only 1–8 larvae (of 100) will survive. Larvae develop by ingesting nurse eggs within the capsules and at 9–12 segments, they leave the capsule and become planktonic (Woodwick 1960).

Larva: The early larval development was described soon after the description of *P. nuchalis* (Woodwick 1960). Trochophore larvae are 180 µm in length at 18 hours and possess rudiments of a prototroch and telotroch, by 72 hours the larva elongates to 200 µm and, although the telotroch is well developed, there is no segmentation. By five days, the larva has two segments, is 260 µm in length, with budding anterior palps and a distinct pygidium. One day later the larva has three segments, three pairs of eyes and begins to feed on nurse eggs. Five segments are reached after one week and 15 by three

weeks (Woodwick 1960). Spionid larvae were collected in plankton samples from under the South Slough Bridge in June in concentrations between 300 to 4000/m³ in February (Blake and Evans 1973). Larvae settle, metamorphose, and begin building tubes at the 13-17 segment stage (Woodwick 1960).

Juvenile

Longevity: The longevity of *Polydora nuchalis* is not known, but its congener *P. ligni* completes a life cycle in 30 days.

Growth Rate:

Food: Individuals collect detritus using long tentacular palps.

Predators:

Behavior:

Bibliography

1. BAILEY-BROCK, J. H. 1990. *Polydora nuchalis* (Polychaeta: Spionidae), a new Hawaiian record from aquaculture ponds. *Pacific Science*. 44:81-87.
2. BLAKE, J. A. 1975. Phylum Annelida: Class Polychaeta, p. 151-243. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
3. —. 1996. Family Spionidae, p. 81-224. *In: Taxonomic atlas of the benthic*

- fauna of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 6. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
4. BLAKE, J. A., and J. W. EVANS. 1973. *Polydora* and related genera as borers in mollusc shells and other calcareous substrates. *Veliger*. 15:235-249.
5. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. Carlton (ed.). University of California Press, Berkeley, CA.
6. WOODWICK, K. H. 1953. *Polydora nuchalis*, a new species of Polycheatous annelid from California. *Journal of the Washington Academy of Science*. 43:381-383.
7. —. 1960. Early larval development of *Polydora nuchalis* Woodwick, a spionid polychaete. *Pacific Science*. 14:122-128.

Upadted 2014

Pseudopolydora kemp

A tube-dwelling sedentary polychaete worm

Phylum: Annelida
Class: Polychaeta
Order: Canalpalpita, Spionida
Family: Spionidae

Taxonomy: *Pseudopolydora kemp* was described by Southern in 1921 from a brackish water lake in India and subsequently found in Japan, for which the subspecies *P. kemp japonica* was later designated by Imajima and Hartman (1964). When this species was found in California, another subspecies was designated (*P. kemp californica*) (Light 1969). However, after re-examining the type specimens of *P. kemp californica*, Blake and Woodwick (1975) determined that the subspecific designations were not necessary and, instead, *P. kemp*, was likely introduced to California from Japan (Carlton 1975; Blake and Woodwick 1975; Light 1978; Cohen and Carlton 1995). Although the species which occurs in Oregon is currently referred to as *P. kemp*, developmental differences suggest that this species is not the same as those from India and Japan (Blake and Ruff 2007).

Description

Size: Individuals up to 28 mm in length (Blake 1975). Our specimens (from Coos Bay) are 16 mm in length and 1.5 mm in width, with nearly 40 segments. Average specimens are 12 mm in length, with 50 body segments (Light 1978).

Color: Pigmentation is variable (Light 1978), but typically pale, with transverse intersegmental rows of black spots anteriorly on most specimens (sp. *kemp*, Blake 1975) (Fig. 3).

General Morphology: Body thickened anteriorly, becoming narrow posteriorly. No division of body into distinct sections. Fifth setiger only slightly modified (Fig. 4).

Body:

Anterior: Prostomium rather blunt, with small bi-lobed lateral horns (Fig. 2). No caruncle, but with

occipital cirrus between palps (Fig. 2).

Trunk:

Posterior: Pygidium cup shaped, flaring and with two dorsal projections or processes (Fig. 4).

Parapodia: Biramous. Anterior noto- and neurosetae include several kinds of capillary and limbate spines (Figs. 5a and b). Notopodial post-setal lobes on setigers 2–5 (Fig. 3). Neuropodial lobes reduced at setiger eight, when they become tori, with hooded hooks.

Setae (chaetae): Modification on setiger five consists of a special J-shaped double row of falcigers (Fig. 5a) (sp. *kemp*, Light 1978), in addition to typical bilimbate setae (Fig. 5b). Setiger one with neurosetal fascicle only, no notosetae (Figs. 2, 3). Posterior neurosetae (from setiger eight) are bidentate hooded hooks in row of 18–20 (Fig. 5c) (genus *Pseudopolydora*, Light 1978).

Eyes/Eyespots: Four small eyes, an outer pair anterior and darker with inner pair subdermal, close together and between palps (Fig. 2).

Anterior Appendages: Anterior with small bi-lobed lateral horns and two conspicuous palps each about 1/3 body length (Fig. 1).

Branchiae: Present on 15–25 segments, beginning on setiger seven (Light 1978) (Figs. 1, 3).

Burrow/Tube: Tube mucoid and animal within is completely hidden, except for extended palps.

Pharynx:

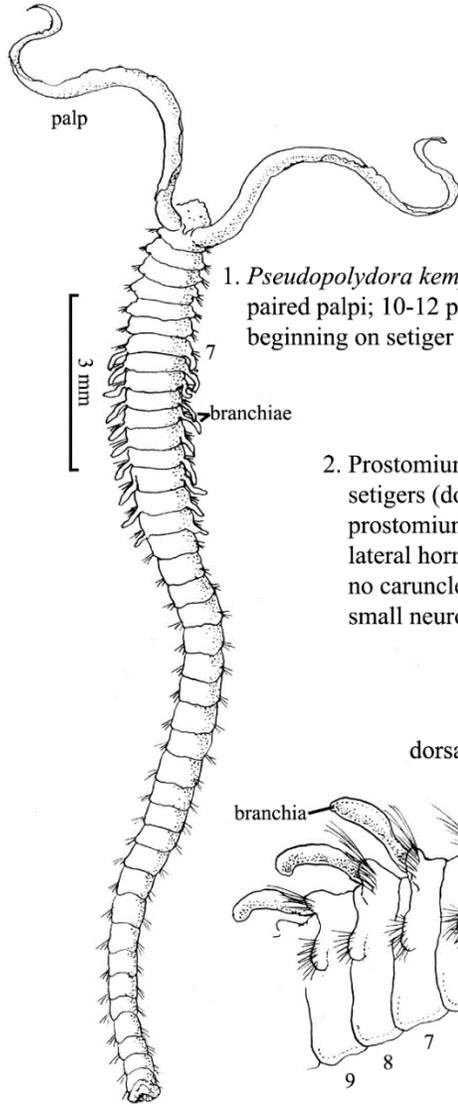
Genitalia:

Nephridia:

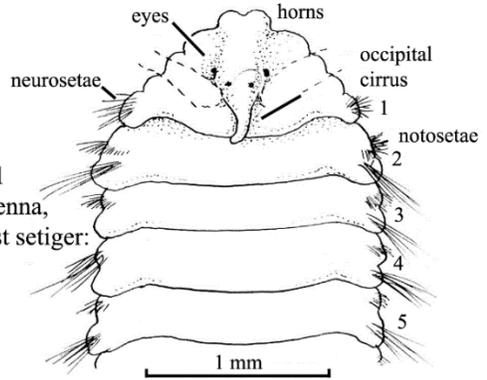
Possible Misidentifications

Spionidae can be distinguished by a pair of long prehensile grooved palps

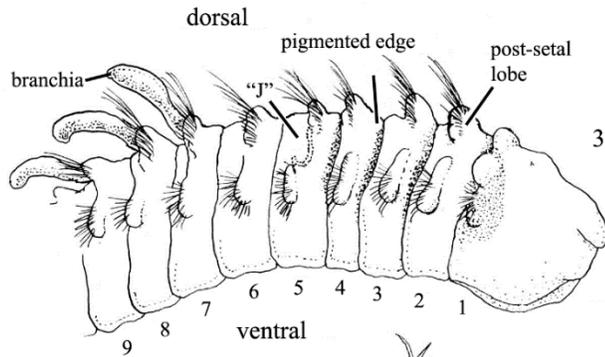
Pseudopolydora kemp



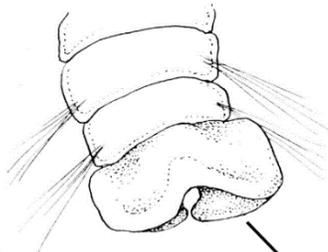
1. *Pseudopolydora kemp* (L:16mm) x10:
paired palpi; 10-12 pairs branchiae,
beginning on setiger 7.



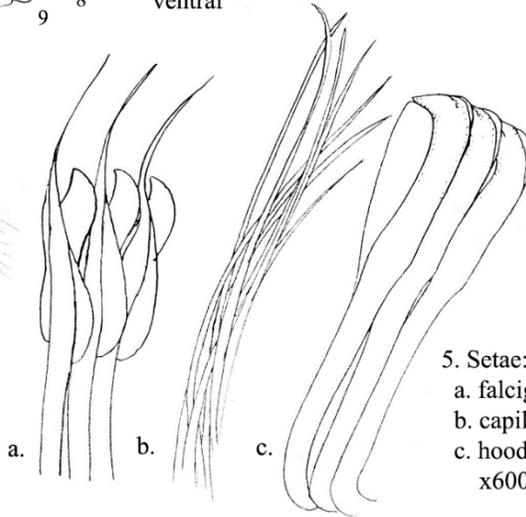
2. Prostomium and anterior
setigers (dorsal view) x30:
prostomium bilobed, small
lateral horns; occipital antenna,
no caruncle; four eyes; first setiger:
small neurosetae only.



3. Anterior (lateral view):
5th setiger with J-shaped
double row of falcigers;
pigmented setiment
edges; branchiae begin on
setiger 7; post-setal lobe
on setigers 2-5.



4. Pygidium (ventral view) x60:
cup-shaped, 2 dorsal processes.



5. Setae:
a. falcigers from 5 x32
b. capillaries from setiger 5 x213
c. hooded hooks from setiger 10
x600.

which arise from the posterior peristomium (Blake 1996). Two other polychaete families have long palps: the Magelonidae, with adhesive palps (not long and flowing) and with flattened spade-like prostomiums and the Chaetopteridae, which have palps, but their bodies are very obviously divided into three quite different regions, which is not the case in spionids. The similar family Cirratulidae, may also have a large pair of palps, but they have tentacular filaments, which are lacking in the spionids. Spionids also have hooded hooks in posterior segments, may or may not have prostomial appendages or branchiae, the prostomium is well developed and fused with peristomium, the pharynx is without jaws and the setae are mostly simple (Blake 1975). Often certain segments are highly modified and have special setae, for example prostomial horns are present in some genera. Spionid parapodia are biramous, with acicula (see *Leitoscoloplos pugettensis*) and sometimes have stout saber setae. There are 19 local spionid genera (Blake and Ruff 2007).

Pseudopolydora spionids can be distinguished from other genera by their unusual J-shaped row of hooks on setiger five (Fig. 3), and by their neuropodial hooded hooks, which begin on setiger eight. *Pseudopolydora* branchiae begin on setiger seven (Fauchald 1977).

Pseudopolydora paucibranchiata is the only other common Pacific Coast species in the genus *Pseudopolydora* (Blake and Ruff 2007). Unlike *P. kemp*, it has a rounded prostomium with no pigment stripes on the anterior segments. Branchiae are present from setiger seven, but there are only 10–12 pairs (Light 1978). The major setae on setiger five are U- or J-shaped (Light 1978), but its pygidium is narrow and cup-like, lacking dorsal projections seen in *P. kemp*. *Pseudopolydora paucibranchiata* is small (4–6 mm, rarely more than 12 mm in length (Light 1978)) and its palps have yellow reflective spots (Blake 1975).

Other genera in this common estuarine family include *Boccardia*, *Polydora* and *Pygospio*. *Boccardia* have branchiae from setiger two and a strongly modified setiger five. *Polydora* also have a strongly modified fifth setiger, their branchiae begin on setiger six and they lack post-setal parapodial lobes (Hartman 1969). *Pygospio* (see *P. elegans*) have branchiae beginning posterior to setiger 10 and the fifth setiger is unmodified. Their tubes are papery and clear, to which fine sand grains adhere.

Ecological Information

Range: Type locality is a brackish water lake in India (Blake and Woodwick 1975). Although it is currently unknown if this species is widely distributed or consists of many cryptic species from distant locations, the current range includes locations in India, South Africa, Kurile Islands and the Pacific coast. California populations were likely introduced with oysters (*Crassostrea*) from Japan in the 1960s (Light 1978).

Local Distribution: Collection sites in Coos Bay include South Slough. Individuals also collected in the Columbia River estuary.

Habitat: Individuals inhabit mucoid tubes in sandy mud of bays and are often found outside beds of the mud shrimp *Callinassa*.

Salinity: Brackish to nearly fresh water with salinity ranging from 6.3–31.9.

Collected at salinities of 30 in Coos Bay.

Temperature: 10–15 °C.

Tidal Level: Intertidal to shallow depths (Hartman 1969) and high intertidal (Coos Bay, South Slough in *Callinassa* beds).

Associates: The amphipod, *Eobrolgus spinosus* is often found within the tubes of *P. kemp*.

Abundance: South Slough, June abundance was measured in cores (15cm diameter x 13 cm depth) at three tidal heights. High intertidal core (1.1 m MLLW) produced 221 animals, mid intertidal (1 m MLLW) produced 4885

animals and low intertidal (0.9 m MLLW), 4113 animals (Posey 1985).

Life-History Information

Reproduction: The reproduction and development of *P. kempfi* has been described and varies with geographic location (Blake and Woodwick 1975; Strikrithnadas and Ramamoorthi 1977; Myohara 1979; Radashevskii 1985; Blake and Ruff 2007). Females brood eggs within capsules that are attached in long strings where the number of eggs per capsule (8–38 to 100–150) and number of capsules per string is highly variable (9–18 to 14–24). Eggs are 99–116 µm (Blake and Arnofsky 1999). California populations have larvae that develop by ingesting nurse eggs, are released from their capsules at the 15-setiger stage and carry out a short pelagic period before settling into the benthos. Populations from India and the Sea of Japan, on the other hand, lack nurse cells, are released at the 3-setiger stage and undergo a long planktotrophic larval stage before settlement (Blake and Ruff 2007).

Larva: The larvae of *P. kempfi* are recognizable by many adult characteristics including a slight modification of the fifth setiger, prominent parapodia, setae both simple and pennoned and arranged in U-shaped rows, and hooded hooks with a secondary tooth close to main fang (Crumrine 2001). Nectochaete larvae are thick and fusiform with metamorphosis occurring at 13–20 setiger stages or 1100–1800 µm in diameter (Blake and Arnofsky 1999). Like developmental mode, larval pigment can vary between populations from California and India and the Sea of Japan (Blake and Ruff 2007).

Juvenile: Metamorphosis is marked by the transition of larval organs to juvenile structures. Anterior feeding palps, for example, which do not process food during larval stages are used for feeding in benthic juveniles and adults. Juvenile palps are long and reach setiger eight. Larval cilia are lost, anterior eyes are

arranged as in adults, prostomium is bifurcate and larval setae are replaced by adult setae. Larval pigment is retained, but gradually lost in developing juveniles. The digestive tract is complete and the pygidium begins as a cup-shaped structure but eventually develops dorsal projections (Blake and Woodwick 1975, Fig. 19–22).

Longevity:

Growth Rate:

Food: Primarily a deposit feeder, but can shift to suspension feeding when water currents increase, by forming palps into helical shapes.

Predators: Fish and shorebirds.

Behavior: When lugworm *Abarenicola* sp. disturbs surface with castings, *Pseudopolydora* can move its tube location (Wilson 1981). Furthermore, the presence or smell of *Abarenicola pacifica* has been shown to reduce settlement of *P. kempfi* juveniles (Woodin 1985).

Bibliography

1. BLAKE, J. A. 1975. Phylum Annelida: Class Polychaeta, p. 151-243. *In*: Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
2. —. 1996. Family Spionidae, p. 81-224. *In*: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 6. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
3. BLAKE, J. A., and P. L. ARNOFSKY. 1999. Reproduction and larval development of the spioniform polychaeta with application to systematics and phylogeny. *Hydrobiologia*. 402:57-106.
4. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In*: Light and Smith manual: intertidal invertebrates from central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.

5. BLAKE, J. A., and K. H. WOODWICK. 1975. Reproduction and larval development of *Pseudopolydora paucibranchiata* (Okuda) and *Pseudopolydora kempfi* (Southern) (Polychaeta: Spionidae). *Biological Bulletin*. 149:109-127.
6. CARLTON, J. T. 1975. Introduced intertidal invertebrates, p. 17-25. *In*: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
7. COHEN, A. N., and J. T. CARLTON. 1995. Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. National Sea Grant Program, Connecticut.
8. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
9. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County Science Series*. 28:1-190.
10. HARTMAN, O. 1969. Atlas of the sedentary polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
11. IMAJIMA, M., and O. HARTMAN. 1964. The polychaetous annelids of Japan. Part II. Allan Hancock Foundation Publications Occasional Papers. 26:239-452.
12. LIGHT, W. J. 1969. *Polydora narica*, new species, and *Pseudopolydora kempfi californica*, new subspecies, two new spionids (Annelida: Polychaeta) from central California. *California Academy of Sciences*.
13. —. 1978. Spionidae: Polychaeta, Annelida. Boxwood Press, Pacific Grove, CA.
14. MYOHARA, M. 1979. Reproduction and development of *Pseudopolydora kempfi japonica* (Polychaeta: Spionidae), with special reference to the polar lobe formation. *Journal of the Faculty of Science Hokkaido University, Series VI. Zoology*. 21:355-364.
15. POSEY, M. H. 1985. The effects upon the macrofaunal community of a dominant burrowing deposit feeder, *Callianassa californiensis*, and the role of predation in determining its intertidal distribution. Ph.D. University of Oregon.
16. RADASHEVSKY, V. I. 1985. The Larval development of the polychaete *Pseudopolydora kempfi japonica* in Peter the Great Bay of the Sea of Japan. *Biologiya Morya-Marine Biology*: 39-46.
17. SRIKRISHNADHAS, B., and K. RAMAMOORTHY. 1977. Development of *Pseudopolydora kempfi* (Southern, 1921) in the laboratory, p. 671-677. *In*: Proceedings of the symposium on warm water zooplankton. Special Publication UNESCO/NIO.
18. WILSON, W. H. 1981. Sediment-mediated interactions in a densely populated infaunal assemblage; the effects of the polychaete *Abarenicola pacifica*. *Journal of Marine Research*. 39:735-748.
19. WOODIN, S. A. 1986. Settlement of infauna: larval choice. *Bulletin of Marine Science*. 39:401-407.

Updated 2014

Pygospio elegans

A spionid polychaete worm

Phylum: Annelida
Class: Polychaeta
Order: Canalpalpita, Spionida
Family: Spionidae

Taxonomy: Several subjective synonyms (synonyms based on individual opinion) are indicated for *Pygospio elegans*, but rarely used (*Spio inversa*, *S. rathbuni*, *S. seticornis* and *Pygospio mimutus*).

Description

Sexual Dimorphism: Males may have small pair of elongated dorsal cirri (sometimes called "auxiliary gills") on setiger two (*Pygospio*, Blake 1975) which are often lost in collection.

Size: Individuals range in size from 10–15 mm in length, having 50–60 segments (Light 1978). This specimen (from Coos Bay) is 5 mm in length, 0.3 mm in width and has 36–37 segments (Fig. 1).

Color: Light, almost white with black markings on anterior segments (Fig. 2), but not on proboscis (Light 1978).

General Morphology: Body slightly flattened dorsolaterally. Fifth setiger normal and not strongly modified as is common among spionids.

Body: The body can be divided into four major regions (from anterior to posterior) including the anterior or head, the thorax and abdomen and, finally, the tail or posterior (Gibson and Harvey 2000).

Anterior: Anterior with two massive short dorsolaterally grooved palps (Figs. 1, 5), which are often lost during collection. Prostomium is without horns, is blunt anteriorly, with lateral swellings and is slightly bi-lobed in some specimens. Anterior is not conical but taper slightly (*sp. elegans*) (Fig. 2). Paired nuchal organs present (Gibson and Harvey 2000, Fig. 1).

Trunk: Thorax with 10–12 abranchiate setigers where each setiger has a dorsal ciliary band and a lateral tuft of cilia. The abdomen is composed of 25–35 setigers where each segment has paired branchiae, a ciliary band (single or double) and two

bands of tufted cilia (Gibson and Harvey 2000).

Posterior: Pygidium with four pigmented conical cirri (*sp. elegans*) (Fig. 3), each possessing inner tufts of cilia (Gibson and Harvey 2000).

Parapodia: Biramous, with cirriform lobes beginning on the second setiger, and diminishing posteriorly. Neuropodia without interramal pouches.

Setae (chaetae): Notopodia with capillary setae only. Neuropodia with simple capillary setae on setigers 1–8 and spoon-like hooded hooks beginning on setigers eight and nine (*sp. elegans*) (Fig. 4).

Eyes/Eyespots: Four eyes present. Anterior pair widely separated and lighter in color than distal pair (Fig. 2). Some individuals have 2–8 eyespots, irregularly arranged along segments (Light 1978).

Anterior Appendages: Two thick grooved palps antero-laterally are used in feeding. They are relatively short and thick as compared to the palps of other spionids.

Branchiae: Numerous branchial pairs, first appearing on setigers 11–13. No branchiae on posterior-most segments.

Burrow/Tube: Tube morphology is species-specific. It is long, papery, clear, covered with fine sand grains and approximately 1 mm in diameter (Bolam 2004) (Fig. 5).

Pharynx: Bears proboscis with a partially eversible conical sac.

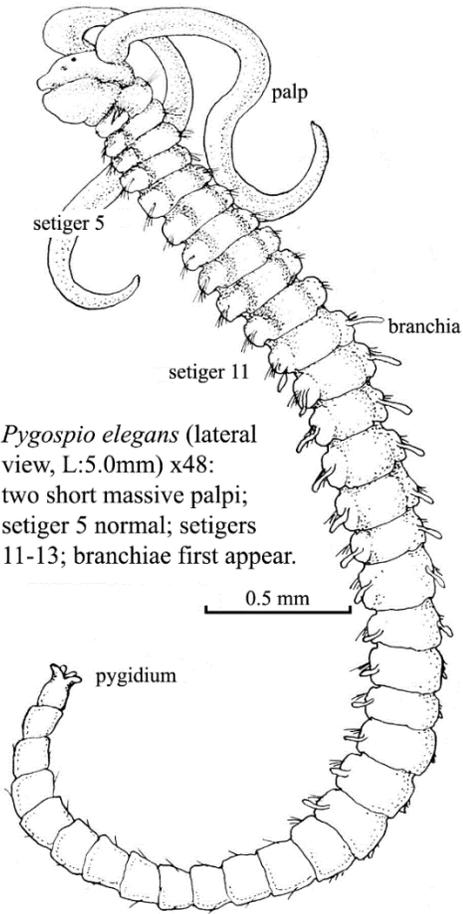
Genitalia:

Nephridia:

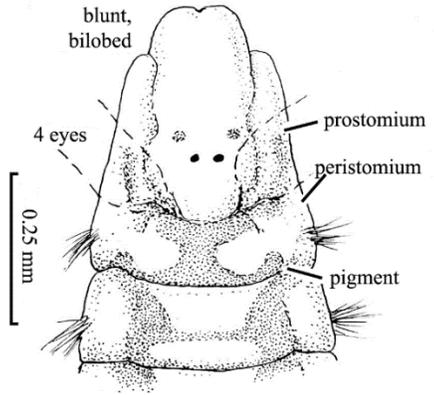
Possible Misidentifications

Spionidae can be distinguished by a pair of long prehensile grooved palps which arise from the posterior peristomium (Blake 1996). Two other polychaete families have long palps: the Magelonidae, with adhesive palps (not long and flowing) and with flattened spade-like prostomiums and the Chaetopteridae, which have palps, but their bodies are very obviously divided into three quite different regions, which is not the case in spionids. The similar family Cirratulidae,

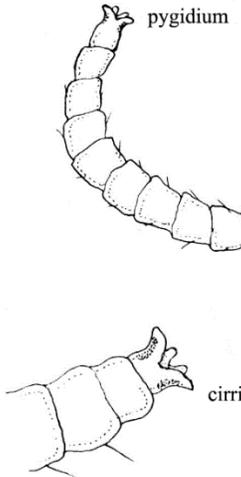
Pygospio elegans



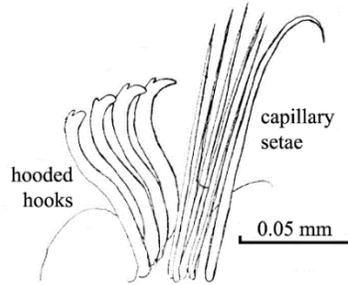
1. *Pygospio elegans* (lateral view, L:5.0mm) x48: two short massive palpi; setiger 5 normal; setigers 11-13; branchiae first appear.



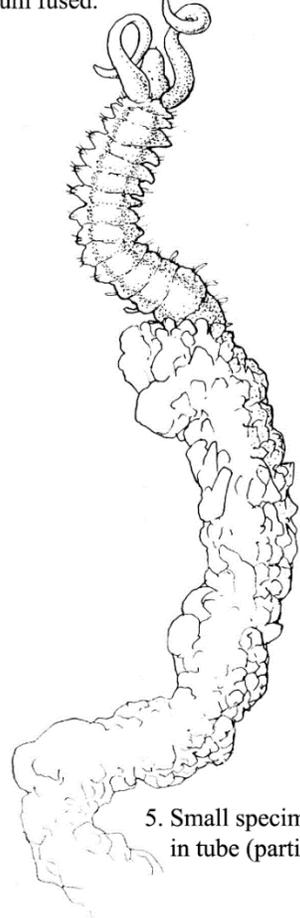
2. Prostomium, anterior segments x100: strong pigment pattern; prostomium, peristomium fused.



3. Pygidium x75: conical cirri.



4. Setae from midsection neuropodium x350.



5. Small specimen in tube (partial) x48.

may also have a large pair of palps, but they have tentacular filaments, which are lacking in the spionids. Spionids also have hooded hooks in posterior segments, may or may not have prostomial appendages or branchiae, the prostomium is well developed and fused with peristomium, the pharynx is without jaws and the setae are mostly simple (Blake 1975). Often certain segments are highly modified and have special setae, for example prostomial horns are present in some genera. Spionid parapodia are biramous, with acicula (see *Leitoscoloplos pugettensis*) and sometimes have stout saber setae. There are 19 local spionid genera (Blake and Ruff 2007).

The genus *Pygospio* is characterized by branchiae beginning posterior to setiger 10 and species lack the dramatically modified fifth setiger of some spionids. *Pygospio californica* is the most closely related species to *P. elegans*. It is green in life and is twice the size of *P. elegans* (Hartman 1969). *Pygospio californica*'s prostomium has a tapered conical tip and is not bi-lobed. Furthermore, *P. californica* has a narrow caruncle that reaches to the first setiger, where *P. elegans* has no caruncle. Brown spots exist on the proboscis in *P. californica* and a reddish brown ventral stripe runs down the first 10–20 segments (Light 1978). The paired branchiae in *P. californica* begin on setiger 19, not on 11–13 as in *P. elegans*. *P. californica* is found on intertidal sand flats and the only record in Oregon is from Umpqua estuary, it is currently only reported from central California (Blake and Ruff 2007).

Other small tube dwelling spionids include the genus *Polydora*, whose tubes are mucoid (Hartman 1969), and *Pseudopolydora kemp*, which also has a mucoid tube, a J-shaped row of falcigers on setiger five and a cup-shaped pygidium.

Ecological Information

Range: Known range includes the northern Atlantic, northern Pacific and western Canada to California (Light 1978).

Local Distribution: Coos Bay collection sites include South Slough. Individuals also collected in the Columbia River estuary.

Habitat: Lives in papery sandy tubes in mud or sand flats and is considered an indicator

species for slight organic pollution (domestic sewage, Germany (Anger 1977)). Their ability to eat suspended as well as deposited matter increases survivability in variable environments (Taghon et al. 1980) (see **Food**).

Salinity: Found at salinities ranging from 30 to 28 in Coos Bay, but also tolerant of salinities as low as 2 (Bolam 2004; Blake 2006).

Temperature:

Tidal Level: Only occurring at high tide level in Coos Bay.

Associates: Associated species include the sabellid polychaete, *Chone ecuadata* (Blake and Ruff 2007).

Abundance: South Slough, June abundance was measured in cores (15 cm diameter x 13 cm depth) at three tidal heights. High intertidal core (1 m MLLW) produced 5–7 animals, mid intertidal (1 m MLLW) produced 6–16 animals and low intertidal (0.9 m MLLW), 13–20 animals. This species is most abundant in April (Posey 1985).

Life-History Information

Reproduction: Both sexual and asexual (by fragmentation or architomy) reproduction have been reported for *P. elegans* (Blake and Arnofsky 1999). Asexual reproduction has been shown to increase in frequency with warmer water temperatures (Armitage 1979; Rasmussen 1953). Spermatophores are mushroom-shaped and have a long tail (Blake and Arnofsky 1999). Eggs are released through nephridial pores into egg capsules within the adult tube (Soderstrom, (Hartman 1941)). Asexual reproduction occurs in March–October while sexual reproduction takes place in winter months (November–December) in False Bay, Washington (Fernald et al. 1987). However, sexual reproduction has been reported in Coos Bay in April. Larvae are adelphophagic, ingesting the unfertilized nurse eggs with which they share a cocoon.

Larva: *Pygospio elegans* larval development proceeds in a variety of ways (as in *Pseudopolydora kemp*) and has been confirmed to be variations across a single species (= poecilogony, Blake and Arnofsky 1999; Morgan et al. 1999; Blake 2006; Kesäniemi et al. 2012). Larvae can ingest nurse eggs and hatch from their capsule at the 3-setiger stage and live as planktonic

larvae before settling at 17–20 setiger stage. On the other hand, larvae can remain in the egg capsule until they are large and hatch out as a non-pelagic larva (Blake 2006, Fig. 13.17). These varying developmental modes may correspond to season, where planktotrophic larvae are more common in spring (Rasmussen 1973; Fernald et al. 1987). Larval characters include, lack of modification on setiger five, prostomium not distally pointed, with frontal horns and branchiae limited to middle and posterior most setigers (except setiger two in males) (Crumrine 2001).

Juvenile:

Longevity: High mortality when disturbed by castings of polychaete *Abarenicola* (Wilson 1981).

Growth Rate: *Pygospio elegans* can fully regenerate their anterior including prostomium and palps in 9–12 days post ablation (Lindsay et al. 2007).

Food: A deposit, suspension and filter feeder, searching mud surface and water for food. Individuals can switch from deposit to suspension feeding when water flow velocity increases (Taghon et al. 1980). A most versatile feeder, *P. elegans* can filter feed by building a mucus net within or above its tube (Fauchald and Jumars 1979; Bolam 2004).

Predators: Fish and shorebirds are major predators because this species lives at high tide level.

Behavior: Moves tube when disturbed by activity of the large lugworm *Abarenicola* sp. (Wilson 1981). Dense patches or aggregations of *P. elegans* are ephemeral, but have a significant effect on the immediate infaunal community (Bolam and Fernandes 2003).

Bibliography

1. ANGER, K. 1977. Benthic invertebrates as indicators of organic pollution in the Western Baltic Sea. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*. 62:245-254.
2. ARMITAGE, D. L. 1979. The Ecology and reproductive cycle of *Pygospio elegans* Claparède (Polychaeta: Spionidae) from Tomales Bay, California: A Thesis. University of the Pacific.
3. BLAKE, J. A. 1975. Phylum Annelida: Class Polychaeta, p. 151-243. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
4. —. 1996. Family Spionidae, p. 81-224. *In: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel*. Vol. 6. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
5. BLAKE, J. A. 2006. Spionida, p. 565-638. *In: Reproductive biology and phylogeny of annelida*. Enfield, Science Publishers. Vol. 4. Science Publishers, Enfield.
6. BLAKE, J. A., and P. L. ARNOFSKY. 1999. Reproduction and larval development of the spioniform polychaeta with application to systematics and phylogeny. *Hydrobiologia*. 402:57-106.
7. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. Carlton (ed.). University of California Press, Berkeley, CA.
8. BOLAM, S. G. 2004. Population structure and reproductive biology of *Pygospio elegans* (Polychaeta: Spionidae) on an intertidal sandflat, Firth of Forth, Scotland. *Invertebrate Biology*. 123:260-268.
9. BOLAM, S. G., and T. F. FERNANDES. 2003. Dense aggregations of *Pygospio elegans* (Claparede): effect on macrofaunal community structure and sediments. *Journal of Sea Research*. 49:171-185.
10. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
11. FAUCHALD, K., and P. A. JUMARS. 1979. Diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology*. 17:193-284.
12. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and

- S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
13. GIBSON, G. D., and J. M. L. HARVEY. 2000. Morphogenesis during asexual reproduction in *Pygospio elegans* Claparede (Annelida, Polychaeta). *Biological Bulletin*. 199:41-49.
 14. HARTMAN, O. 1941. Polychaetous annelids. Part III. Spionidae. Some contributions to the biology and life history of Spionidae from California. Allan Hancock Foundation of Scientific Research. Allan Hancock Pacific Expeditions. Reports. 7:299.
 15. —. 1969. Atlas of the sedentariate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
 16. KESÄNIEMI, J. E., P. D. RAWSON, S. M. LINDSAY, and K. E. KNOTT. 2012. Phylogenetic analysis of cryptic speciation in the polychaete *Pygospio elegans*. *Ecology and Evolution*. 2:994-1007.
 17. LIGHT, W. J. 1978. Spionidae: Polychaeta, Annelida. Boxwood Press, Pacific Grove, CA.
 18. LINDSAY, S. M., J. L. JACKSON, and S. Q. HE. 2007. Anterior regeneration in the spionid polychaetes *Dipolydora quadrilobata* and *Pygospio elegans*. *Marine Biology*. 150:1161-1172.
 19. MORGAN, T. S., A. D. ROGERS, G. L. J. PATERSON, L. E. HAWKINS, and M. SHEADER. 1999. Evidence for poecilogony in *Pygospio elegans* (Polychaeta: Spionidae). *Marine Ecology Progress Series*. 178:121-132.
 20. POSEY, M. H. 1985. The effects upon the macrofaunal community of a dominant burrowing deposit feeder, *Callianassa californiensis*, and the role of predation in determining its intertidal distribution. Ph.D. University of Oregon.
 21. RASMUSSEN, E. 1953. Asexual reproduction in *Pygospio elegans* Claparède (Polychaeta sedentaria). *Nature*. 171:1161-1162.
 22. —. 1973. Systematics and ecology of the Isefjord marine fauna (Denmark) with a survey of the eelgrass (*Zostera*) vegetation and its communities. *Ophelia*. 11:1-507.
 23. TAGHON, G. L., A. R. NOWELL, and P. A. JUMARS. 1980. Induction of suspension feeding in spionid polychaetes by high particulate fluxes. *Science (New York, N.Y.)*. 210:562-4.
 24. WILSON, W. H. 1981. Sediment-mediated interactions in a densely populated infaunal assemblage; the effects of the polychaete *Abarenicola pacifica*. *Journal of Marine Research*. 39:735-748.

Updated 2014

Scolelepis foliosa

A very large spionid polychaete

Phylum: Annelida
Class: Polychaeta
Order: Canalpalpita, Spionida
Family: Spionidae

Taxonomy: The taxonomic history of this species is extensive and has yet to be fully resolved. The genus *Scolelepis* has many synonyms including *Aonis*, *Nerine*, *Pseudomalacoceros*, *Nerinides*, *Scolecopsis* and *Pseudonerine* (Pettibone 1963). Furthermore, several subgenera have been proposed for *Scolelepis*. In 1963, Pettibone suggested the subgenera *Scolelepis* and *Nerinides* based on neuropodial lamellae and ventral cirri. In 1987, Maciolek suggested the subgenera *Scolelepis* and *Parascolelepis* based on hooded hook morphology. These subgenera were then erected to generic status by Williams (2007) based on the phylogenetic analysis of Blake and Arnofsky (1999) (Blake 2006; Rocha and de Paiva 2012). The genus *Scolelepis* now includes 45 species (Delgado-Blas 2006; Rocha and de Paiva 2012). *Scolelepis foliosa* has many synonyms including *Aonis foliosa*, *Nerine coniocephala*, *Aonis vittata*, *Nerine sarsiana* and *Nerine foliosa occidentalis* and may be the same species as *S. alaskensis* and *S. bonnieri* (Treadwell 1914; Pettibone 1963).

Description

Size: The illustrated specimen (from Coos Bay) is 500 mm in length and 15 mm in width, with over 500 segments. The first 130 segments are 140 mm in length. *Scolelepis alaskensis*, which may be the same species, has 130 segments and is 80 mm in length (Treadwell 1914).

Color: The specimens we examined are golden tan with green palps that have white lines and spots, and red vessels.

General Morphology: A large and thick worm that is rectangular in cross section and bears many tightly arranged segments (Fig. 1).

Body: Not divided into distinct body regions (Spionidae) (Blake 1996).

Anterior: Prostomium pointed and tapered anteriorly (*Scolelepis*, Light 1978; Pettibone 1963), but can also be

rounded (Berkeley and Berkeley 1952; Hobson and Banse 1981) (Fig. 2b). No frontal horns. Small occipital cirrus present (Fig. 2a) and no caruncle (= dorsal sense organ, Hobson and Banse 1981) (Fig. 2b). Peristomium enlarged and envelops prostomium with two rolls (Light 1978) (Fig. 2b).

Trunk: Fifth setiger not modified (Figs. 1, 2a) and no interparapodial pouches (brackets, Fig. 1) (genus *Scolelepis*).

Posterior: Anus and pygidium are dorsal (Fig. 3). Pygidium is a thick, lobed pad with no cirri.

Parapodia: Biramous, lamellar and with variable shape (Fig. 5). Podia become small toward worm posterior (Fig. 5d), but are not glandular or thick.

Setae (chaetae): Fine spines (capillaries) in all noto- and neuropodia. Hooded hooks (Fig. 4a) begin in neuropodia after setiger 57 (sp. *foliosa*, Light 1978). Hooks also on notopodia on posterior-most setigers (Figs. 4, 5c, d). Hooks hooded, unidentate or multidentate and worn (Fig. 4a). Capillary setae limbate (no wings) and very finely striated, some with horizontal ribs begin at setiger 39 (Fig. 4b). Notosetae present in setiger one (Fig. 2a). No setae with distal fringe.

Eyes/Eyespots: Two pairs, anteriorly, in some specimens (not the present specimen).

Anterior Appendages: Simple, massive and long (extending to setiger 20). Feeding palps (Fig. 1) are easily broken off.

Branchiae: Branchiae are long, cirriform and partly fused to parapodial lamellae, begin on setiger two (Figs. 2a, b) and continue almost to the worm posterior (genus *Scolelepis*, Light 1978) (Fig. 1).

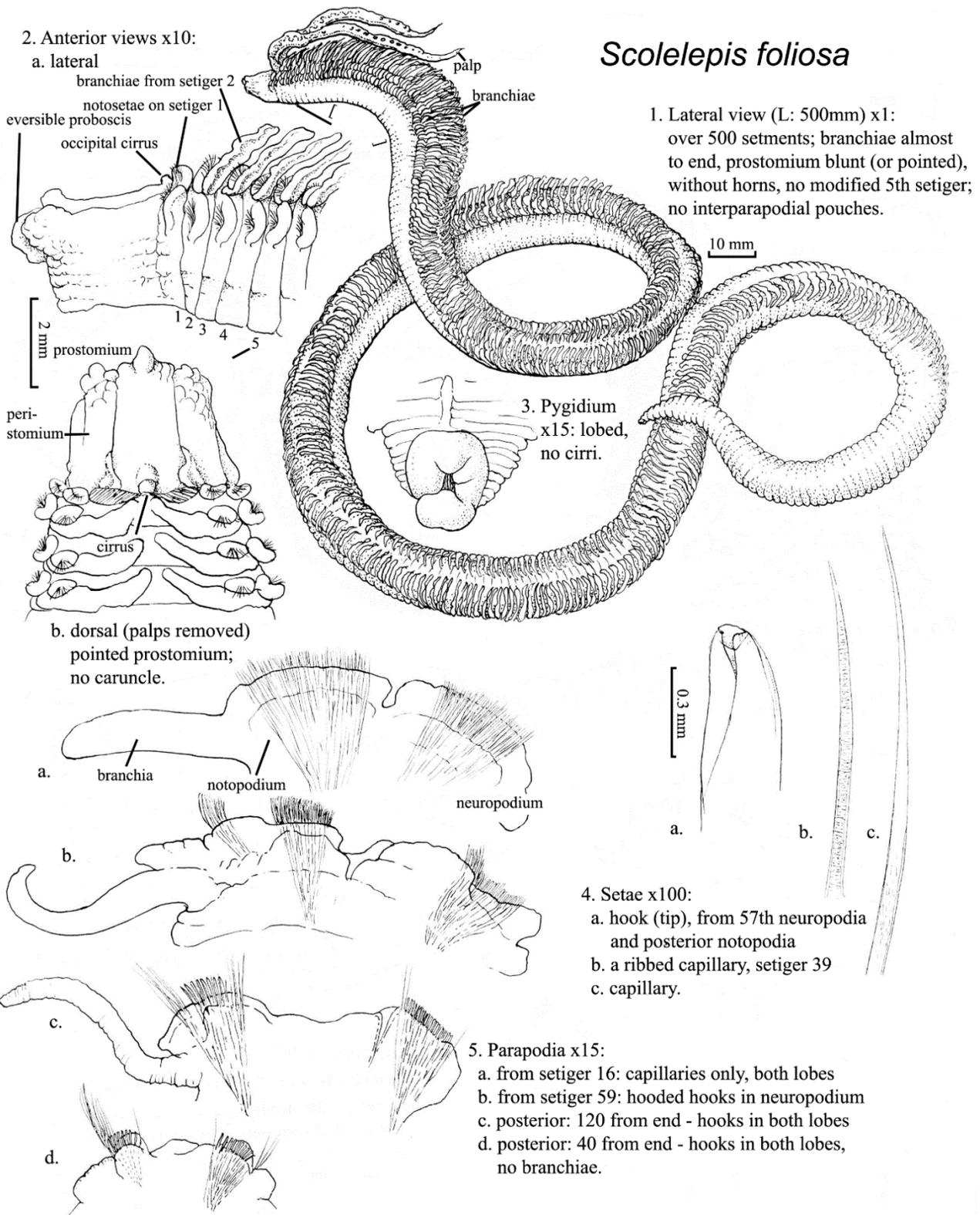
Burrow/Tube: Individuals make loose vertical burrows in shifting sands, but have no permanent tube (Pettibone 1963).

Pharynx: Bears a large, eversible proboscis which is saclike.

Genitalia:

Nephridia:

Scolelepis foliosa



2. Anterior views x10:

a. lateral

branchiae from setiger 2
 notosetae on setiger 1
 eversible proboscis
 occipital cirrus
 1 2 3 4 5
 prostomium
 2 mm

peri-stomium

cirrus

b. dorsal (palps removed)
 pointed prostomium;
 no caruncle.

a.

branchia

notopodium

neuropodium

b.

c.

d.

1. Lateral view (L: 500mm) x1:
 over 500 setments; branchiae almost
 to end, prostomium blunt (or pointed),
 without horns, no modified 5th setiger;
 no interparapodial pouches.

10 mm

3. Pygidium
 x15: lobed,
 no cirri.

0.3 mm

a.

b.

c.

4. Setae x100:

- a. hook (tip), from 57th neuropodia and posterior notopodia
- b. a ribbed capillary, setiger 39
- c. capillary.

5. Parapodia x15:

- a. from setiger 16: capillaries only, both lobes
- b. from setiger 59: hooded hooks in neuropodium
- c. posterior: 120 from end - hooks in both lobes
- d. posterior: 40 from end - hooks in both lobes, no branchiae.

Possible Misidentifications

Spionidae can be distinguished by a pair of long prehensile grooved palps which arise from the posterior peristomium (Blake 1996). Two other polychaete families have long palps: the Magelonidae (adhesive palps, not long and flowing, and flattened spade-like prostomiums) and the Chaetopteridae (have palps, but their bodies are very obviously divided into three quite different regions which is not the case in spionids). The similar family Cirratulidae, may also have a large pair of palps, but they have tentacular filaments, which are lacking in the spionids. Spionids also have hooded hooks in posterior segments, may or may not have prostomial appendages or branchiae, the prostomium is well developed and fused with peristomium, the pharynx is without jaws and the setae are mostly simple (Blake 1975). Often certain segments are highly modified and have special setae, for example prostomial horns are present in some genera (not *Scolelepis*). Spionid parapodia are biramous, with acicula (see *Leitoscoloplos pugettensis*) and sometimes have stout saber setae (not *Scolelepis*). There are 19 local spionid genera (Blake and Ruff 2007).

Several other, locally occurring genera of spionids have well developed branchiae and pointed prostomia. *Spio* also has branchiae from setiger one, but lacks accessory branchiae. In *Pygospio*, branchiae first appear on setiger 10. (Males have an additional pair on setiger two (Light 1978). In both genera *Malacoceros* and *Laonice* the branchiae begin on setiger two. *Malacoceros* species are distinct in having ventral saber setae on their median and posterior segments and a prostomium with horns (Light 1978). *Laonice* lack the horns and saber setae, but have a very long caruncle, interparapodial pouches, and anal cirri. They also have branchiae only on the anterior segments – all characteristics that are lacking in *Scolelepis*.

The genus *Scolelepis* is characterized by its pointed prostomium (which is blunt in *S. foliosa*), a caruncle (if present) to setiger two, a possible occipital cirrus, cirriform branchiae beginning on setiger two, an unmodified fifth setiger, no interparapodial pouches or saber setae and a pad-like

pygidium (Light 1978). Other species that could be found in our area include:

Scolelepis squamata, a species referred to as *Nerinides acuta* when it was found in San Francisco Bay (Jones 1961) and as *Nerine cirratulus* in South Slough, Coos Bay (Hartman and Reish 1950) as well as other places (Berkeley and Berkeley 1952; Hartman 1969). This species also has many synonyms (*Spio acuta*, *Nerine minuta*, and *Nerine agilis*) (Light 1978) and is primarily distinguishable from *S. foliosa* by its hooded hooks, which appear first on setigers 25–40 and not on setiger 57. Other differences include its capillary setae, which are limbate and without ribs. The prostomium of *S. squamata* is pointed fore and aft and it usually possesses two pairs of eyes. *Scolelepis squamata* can be up to 80 mm in length and have up to 200 segments (Light 1978). Unlike *S. foliosa*, it has no occipital cirrus, and it does have a caruncle to setiger two. Like *S. foliosa*, it has long cirriform branchiae from setiger two and the post-setal lamellae of setiger one are well developed.

Scolelepis tridentata has been found in California and in Ireland. It is not known if it is present in Oregon. It has tridentate hooded hooks, each with a large central fang, which begin on setigers 15–16, not on setiger 57. Capillary setae are limbate (unlike in *S. foliosa*), but are similarly ribbed.

Scolelepis texana is reported from central CA and the eastern United States including the Gulf of Mexico. This species is recognizable by the lack of notosetae on the first setiger and neuropodial hooded hooks from setigers 13–27 (Blake and Ruff 2007).

Ecological Information

Range: *Scolelepis foliosa* exhibits a cosmopolitan distribution, which may be due in part to its convoluted taxonomic history and extensive synonymies. Pacific Coast range includes British Columbia (Berkeley and Berkeley 1952) and Washington (Imajima and Hartman 1964). Individuals are reported from Oregon and California (as *S. f. occidentafis*) by Audouin and Milne-Edwards 1833, although this species is not currently included in the most recent intertidal guide (Blake and Ruff 2007).

Local Distribution: Distribution in Coos Bay includes Clam Island, Pigeon Point, Charleston mudflats (e.g., Portside) and bay mouth, subtidally.

Habitat: Loose sandy mud and gravel in Coos Bay. Offshore in clean well-sorted sand (Hancock et al. 1984).

Salinity: Specimens collected at 30.

Temperature: Ranges from 9–15 °C.

Tidal Level: Found at approximately 0.0 m at Pigeon Point in Coos Bay. Offshore in about 5.4 m (Hancock et al. 1984).

Associates:

Abundance: Not common in Coos Bay.

Life-History Information

Reproduction: Pelagic development where larvae are mostly planktotrophic (Hannerz 1956).

Larva: Larvae of *Scolelepis foliosa* are planktotrophic and can be recognized using many adult characters including the presence of branchiae, setiger one and setiger five not modified and without specialized setae (as in adults), a pointed and triangular prostomium that may or may not bear lateral horns and a blackish brown gut (Crumrine 2001).

Juvenile:

Longevity:

Growth Rate:

Food: Selective surface deposit feeder (Fauchald and Jumars 1979).

Predators:

Behavior:

Bibliography

1. AUDOUIN, J. F., and H. MILNE-EDWARDS. 1833. Classification des annelides et description de celles qui habitent les cotes de la France. *Annales Des Sciences Naturelles*. 80:411-425.
2. BERKELEY, E., and C. BERKELEY. 1952. Annelida. Polychaeta sedentaria. *Canadian Pacific Fauna*. 9b:1-139.
3. BLAKE, J. 2006. Spionida, p. 565-638. *In: Reproductive biology and phylogeny of annelida*. Enfield, Science Publishers. Vol. 4. Science Publishers, Enfield.
4. BLAKE, J. A. 1975. Phylum Annelida: Class Polychaeta, p. 151-243. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
5. —. 1996. Family Spionidae, p. 81-224. *In: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel*. Vol. 6. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
6. BLAKE, J. A., and P. L. ARNOFSKY. 1999. Reproduction and larval development of the spioniform polychaeta with application to systematics and phylogeny. *Hydrobiologia*. 402:57-106.
7. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. Carlton (ed.). University of California Press, Berkeley, CA.
8. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
9. DELGADO-BIAS, V. H. 2006. Partial revision of *Scolelepis* (Polychaeta : Spionidae) from the Grand Caribbean Region, with the description of two new species and a key to species recorded in the area. *Contributions to Zoology*. 75:75-97.
10. FAUCHALD, K., and P. A. JUMARS. 1979. Diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology*. 17:193-284.
11. HANCOCK, D. R., P. O. NELSON, C. K. SOLLITT, and K. J. WILLIAMSON. 1984. Coos Bay offshore disposal site investigation: interim report phase I, February, 1979-March, 1980, Portland, OR.
12. HANNERZ, L. 1956. Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil, and Poecilochaetidae N. fam: in the Gullmar Fjord (Sweden), p. 204. *In: Zoologiska bidrag fran Uppsala*. Uppsala University, Uppsala, Sweden.
13. HARTMAN, O. 1969. Atlas of the sedentariate polychaetous Annelids

- from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
14. HARTMAN, O., and D. J. REISH. 1950. The Marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
 15. HOBSON, K. D., and K. BANSE. 1981. Sedentariate and archiannelid polychaetes of British Columbia and Washington. Canadian Bulletin of Fisheries and Aquatic Sciences. 209:1-144.
 16. IMAJIMA, M., and O. HARTMAN. 1964. The polychaetous annelids of Japan. Part II. Allan Hancock Foundation Publications Occasional Papers. 26:239-452.
 17. JONES, M. L. 1961. A quantitative evaluation of the benthic fauna off Point Richmond, California. University of California. Publications in Zoology. 67:219-320.
 18. LIGHT, W. J. 1978. Spionidae: Polychaeta, Annelida. Boxwood Press, Pacific Grove, CA.
 19. MACIOLEK, N. 1987. New species and records of *Scolelepis* (Polychaeta: Spionidae) from the east coast of North America, with a review of the subgenera. Proceedings of the Biological Society of Washington. 7:16-40.
 20. PETTIBONE, M. H. 1963. Revision of some genera of polychaete worms of the family Spionidae, including the description of a new species of *Scolelepis*. Proceedings of the Biological Society of Washington. 76:89-103.
 21. ROCHA, M. B., and P. C. DE PAIVA. 2012. *Scolelepis* (Polychaeta: Spionidae) from the Brazilian coast with a diagnosis of the genus. Zoologia. 29:385-393.
 22. TREADWELL, A. L. 1914. Polychaetous annelids of the Pacific Coast in the collections of the Zoological museum of the University of California. University of California Publications in Zoology. 13.
 23. WILLIAMS, J. D. 2007. New records and description of four new species of Spionids (Annelida: Polychaeta: Spionidae) from the Philippines: the genera *Dispio*, *Malacoceros*, *Polydora*, and *Scolelepis*, with notes on palp ciliation patterns of the genus *Scolelepis*. Zootaxa. 1-35.

Updated 2014

Hobsonia florida

A tube-dwelling polychaete worm

Phylum: Annelida
Class: Polychaeta
Order: Terebellida
Family: Ampharetidae

Taxonomy: *Hobsonia florida* was originally described as *Amphicteis gunneri floridus* by Hartman (1951) and, after examination of paratypes, was synonymized with *Hypaniola grayi* (Pettibone, 1953) which was later included with *Amphisomytha* in the genus *Lysippides* (Day, 1964). Zottoli (1974) separated *Amphicteis gunneri floridus* into two species: *A. gunneri* and *A. floridus* based on the number of nephridial pairs, abdominal segments, lack of anal cirri and lack of rudimentary notopodia on abdominal segments. This species was then moved to the newly designated genus, *Hobsonia* in 1979 (Banse). Banse recognized this new genus based on a unique combination of external characters and internal anatomy and provides characters against it being a member of *Hypaniola*, *Amphicteis* or *Lysippides* (Banse 1979).

Description

Size: Individuals range in length from 8–15 mm (Zottoli 1974). The specimens on which we base this description are up to 12 mm in length and 1.5 in width (from the Columbia River).

Color: Orange with whitish spots (Banse 1979). White when preserved.

General Morphology: Rather conical and large anteriorly, becoming small at posterior end. Conspicuous thoracic dorsal to ventral transition (Fig. 1).

Body: Approximately 43 segments with eight smooth cylindrical branchiae, snout-like prostomium. Fine paleae anteriorly, capillary notosetae and uncinigerous neurosetae present (Fig. 3).

Anterior: Prostomium has four lobes and is well developed and prolonged into a snout (Hartman 1951). Lobes may be more noticeable in preserved specimens, as some live animals are

smooth (Pettibone 1953). Glandular ridges present, but not in all specimens (Banse 1979).

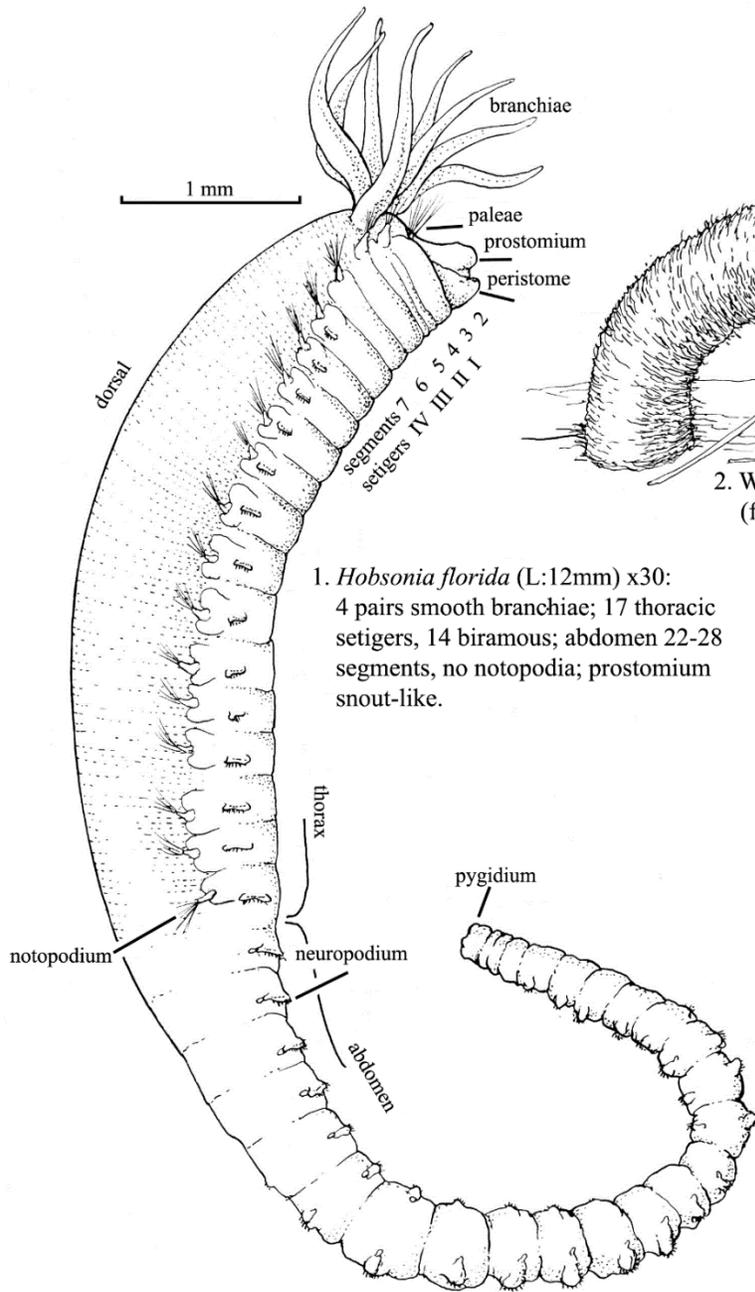
Trunk: Thorax is stout, with 17 setigerous segments and two anterior asegmentous segments (Fig. 1). Abdomen is with 22–28 segments (species *florida*, Zottoli 1974) (23–26 segments, genus *Hobsonia*, Banse 1979). Abdomen has neuropodia only, no notopodia. Instead, only rudimentary lobes in anterior segments (species *florida*, Banse 1979) (Fig. 1). Abdomen narrow and reduced. Dissected specimens with 26 segments where 23 are setigerous and the last three are without setae (Fig. 1).

Posterior: Pygidium without anal cirri or papillae (species *florida*, Zottoli 1974) and is slightly lobed. Posterior segments can be turned inward. A pair of eyespots in young at posterior end of worm are visible in live specimens and in some freshly preserved adults (Banse 1979), but were not observed in the illustrated specimen.

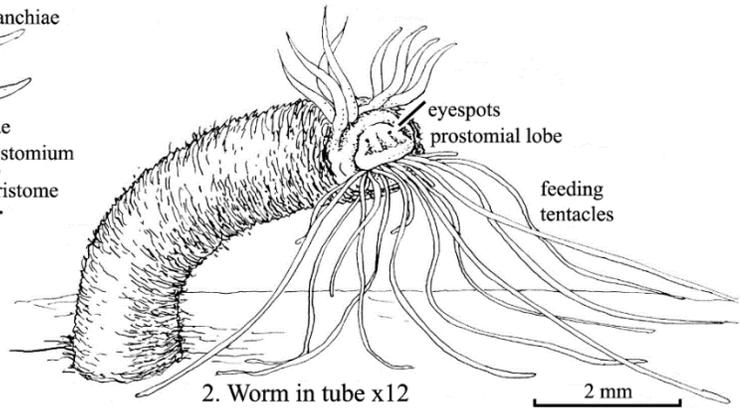
Parapodia: Reduced and biramous in thorax. Uniramous neuropodia only in abdomen (Fig. 1). Seventeen notopodia begin on segment four (Pettibone 1953) and each consists of a single lobe with a fascicle of capillary setae (Fig. 3a). Notopodium with a small cirrus. Fourteen thoracic neuropodia and 23 abdominal. Thoracic neuropodia begin on segment seven (setiger four) (Pettibone 1953) and each is made up of a single row of uncini in a torus (Fig. 1, 4). Thoracic uncini have four teeth and abdominal uncini have five (Fig. 3c) (Pettibone 1953). A long dorsal cirrus is present on abdominal neuropodia (Banse 1979) (Fig. 4).

Setae (chaetae): Fascicles of about eight (on each side) fine and flattened setae on segment three (Banse 1979) with delicate

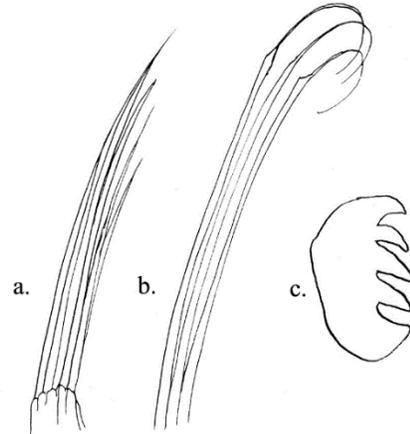
Hobsonia florida



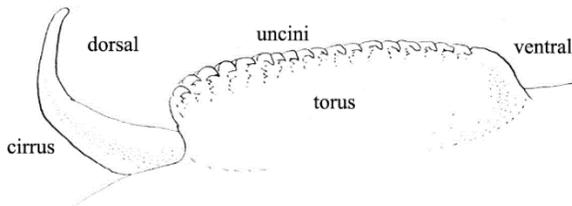
1. *Hobsonia florida* (L:12mm) x30:
4 pairs smooth branchiae; 17 thoracic setigers, 14 biramous; abdomen 22-28 segments, no notopodia; prostomium snout-like.



2. Worm in tube x12
(from Fauchald & Jumars, 1979).



3. Setae:
a. capillary notosetae x150 from setiger 8; 6 in fascicle;
b. paleae x100 from segment 2;
c. uncinus (neuropodial) x1000 (abdominal-5 teeth).



4. Neuropodium x400:
from abdominal setiger 4
long dorsal cirrus.

flexed tip (Fig. 1, 3b). Paleae are not much more obvious than capillary notosetae.

Eyes/Eyespots: Two small eyes behind glandular ridges on prostomium (Fig. 2) are observed in preserved specimens. Live animals can have clusters of pigment spots on the underside of upper lip (Banse 1979).

Anterior Appendages: Up to 20 feeding tentacles that are fine, grooved and transparent. Lateral feeding tentacles are shorter than ventral ones (Fig. 2). Tentacles are very distensible and retractile into mouth (Ampharetidae, Kozloff 1974; Blake 1975) and can be as long as the worm (Banse 1979). No palps or other prostomial appendages (Fig. 2).

Branchiae: Dorsal branchiae can have white transverse pigment bands, making them appear to be jointed (Fauchald and Jumars 1979) (not observed in the illustrated specimen). There are four branchial pairs which are cylindrical, smooth and pointed. The first pair is attached to segment three (the segment bearing paleae) and subsequent pairs are attached to segments 3–5 (Fig. 1).

Burrow/Tube: A mucus-lined tube composed of sediment particles and debris on the outside which gives the tube a shaggy, annulated appearance (Fig. 2). Tube length is about five times worm body length and the upper 1/3 projects above substrate (Zottoli 1974). Juveniles build first tubes a few days after settling (Fauchald and Jumars 1979).

Pharynx:

Genitalia:

Nephridia: Two pairs of long nephridia are present in segments six and seven (Banse 1979).

Possible Misidentifications

Ampharetidae are small worms, usually less than 5 cm long (Kozloff 1974), with clearly defined thorax and abdomen, both of which have neuropodia with uncini. The notosetae are capillary in the thorax and are reduced or absent in the abdomen (Fauchald 1977). They have two to four pairs of simple branchiae, and completely retractable feeding tentacles (Blake 1975). There are numerous ampharetid genera and many of them are deepwater inhabitants. Some of the intertidal and shallow water genera include:

Amage (Malmgren, 1866) has been found in Puget Sound (Banse 1979). This genus lacks paleae, unlike *Hobsonia*. Like *Hobsonia*, it has smooth branchiae, which are all of 1 type (Kozloff 1974).

Ampharete sp. have 14 thoracic setigers (not 17, as in *Hobsonia*). Like *Hobsonia*, *Ampharete labrops* (Hartman, 1951), widespread in California (Blake and Ruff 2007), has four pairs of smooth branchiae (Blake 1975), but the latter species can be differentiated because it has numerous eyespots on the margin of its large upper lip, as well as two small ones on the upper side. It has 13 abdominal uncinigers and two anal cirri. *Ampharete arctica* (Malmgren, 1866), native to Norway (Hartman 1969) is found in Puget Sound (Kozloff 1974). Its four pairs of branchiae are in two rows: three pairs in the first row and one pair in the second row near the midline. *Ampharete acutifrons* (Grube, 1860) has been reported from Alaska, British Columbia, and Washington, and has long anal cirri (Banse 1979). Its four pairs of branchiae are also in two rows where there are two pairs in each row (Gallagher 1979).

Anobothrus sp. has four pairs of branchiae and anterior paleae (like *Hobsonia*), but has only 15 thoracic setigers and 12 uncinigers (*H. florida* has 17 and 14, respectively). It has one thoracic setiger (setiger 10 or 11) with elevated and modified notosetae (Fauchald 1977).

Hypaniola kowalewskii (Grimm in Annenkova, 1972) possibly found only in Europe. Like *Hobsonia*, it has four pairs of smooth branchiae and small paleae. Unlike *Hobsonia*, this currently monotypic genus (Fauchald 1977) lacks glandular prostomial ridges.

Melinna species are similar to *Hobsonia* in having four pairs of smooth branchiae and only 14 thoracic uncinigers. Unlike *Hobsonia*, *Melinna* has nuchal hooks anterior to the branchiae and a dorsal crest on segment six. *Melinna oculata* is found from central California to Oregon, but is subtidal (Blake and Ruff 2007). *Melinna elizabethae* is found in the Arctic and northeastern Pacific (Banse 1979).

Schistocomus hiltoni (Chamberlin, 1919) is the most common local form (Blake 1975)

and has 15 thoracic setigers and lacks paleae. *Schistomocomus hiltoni* has only 15 thoracic setigers and three pairs of pinnate and one pair of smooth branchiae. In *H. florida* the branchiae are all smooth and there are 17 thoracic setigers. It is found most often on open coasts (Blake 1975).

The genus *Hobsonia* (Banse, 1979) is distinguished by its lack of anal cirri, its great number of abdominal segments (23-26) and its lack of all but rudimentary notopodial lobes in the abdomen (Banse 1979).

Ecological Information

Range: Type locality is off the coast of Florida in the Gulf of Mexico (Hartman 1951) and *Hobsonia florida* is a common non-indigenous species to the NE Pacific (Castillo et al. 2000) where its range extends from British Columbia to Washington and Oregon (Banse 1979).

Local Distribution: Oregon sites include the Columbia River, Young's and Yaquina Bay (Castillo et al. 2000), Astoria, Siletz and Salmon Rivers.

Habitat: Salt marshes near river mouths in intertidal and subtidal estuarine mud (Zottoli 1974; Banse 1979). Worms live in tubes projecting obliquely above surface where orientation depends on available food (Fauchald and Jumars 1979).

Salinity: Salinity can range from 0–27 (Zottoli 1974). Juveniles can reach sexual maturity in areas of low salinity (Banse 1979). *Hobsonia florida* has been collected in Long Island Sound, New York at salinities ranging from 4–8 (Olson et al. 2009).

Temperature: Larvae were reared at temperatures ranging from 20–30°C (Zottoli 1974).

Tidal Level: Intertidal and subtidal.

Associates: Common associates include the amphipod, *Corophium salmonis*, which replaces *H. florida* in succession (Gallagher 1979). Atlantic coast associates include polychaetes in the genera *Leitoscoloplos*, *Heteromastus*, *Polydora*.

Abundance: Densities reached 150/10 cm² in Skagit, Washington three weeks after colonization (Gallagher 1979).

Life-History Information

Reproduction: Spawning from late May to early September (New Hampshire, Zottoli 1974). Females release eggs (approximately

100) which are fertilized within the tube from sperm moved into the tube by ciliary currents (Blake 2000). Irregularly-shaped eggs, each approximately 200 µm in diameter (Washington, Banse 1979), do not develop inside a sac, but are lost within the tube. The female remains inside the tube during their development (Zottoli 1974).

Larva: The development and larvae of *Hobsonia florida* (= *Amphicteis floridus*) were described by Zottoli (1974). Larvae remain in the tube until the three-setiger stage (two days) and settle into the benthos where they immediately build their own tubes (Olson et al. 2009). Early larvae have notosetae that are spatulate and are replaced by capillary setae and a single anterior tentacle. All tentacles are developed once the larva reaches six-setiger stage and they are used in feeding by the eight-setiger stage. At 11 segments, branchiae are apparent and develop sequentially, such that all three pairs are present when the worms are 18 segments in length. Once the larva has 16–17 segments its uncini are patterned as in adults (Blake 2000; Olson et al. 2009).

Juvenile: Newly recruited juveniles are 200 µm (Gallagher et al. 1983).

Longevity:

Growth Rate: Growth from one to 18 setigers in 36 days. Branchiae develop by 11-setiger stage and larvae are easily raised in the lab (Zottoli 1974). *Hobsonia florida* are among the earliest colonist in succession (e.g. sand flats, Skagit, Washington). When a population crashes, it is replaced by amphipods and other polychaetes (Gallagher 1979).

Food: A surface deposit feeder, *H. florida* picks up particles with feeding tentacles. Ampharetids eats detritus, unicellular algae and larval invertebrates (Fauchald and Jumars 1979). Worms begin feeding as newly settled juveniles of 2–3 setigers, by muscular pumping of lips, before tentacles develop (Zottoli 1974). When feeding, an adult stretches out of tube, spreads tentacles over substratum and suspends branchiae in water (Fauchald and Jumars 1979) (Fig. 2). Food ingestion and particle selection is dependent on particle surface texture and size. Research suggests that particles are sorted on the basis of specific gravity once in the gut (Self and Jumars 1978).

Predators: The amphipod *Eogammarus confervicolus* preys on juvenile *Hobsonia florida* (Gallagher 1979).

Behavior: Mostly sessile, but moves by continuous tube-building especially when food is scarce (Fauchald and Jumars 1979).

Bibliography

1. BANSE, K. 1979. Ampharetidae (Polychaeta) from British Columbia and Washington. *Canadian Journal of Zoology*. 57:1543-1552.
2. BLAKE, J. A. 1975. Phylum Annelida: Class Polychaeta, p. 151-243. *In*: Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
3. —. 2000. Family Ampharetidae, p. 97-150. *In*: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 7. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
4. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In*: Light and Smith manual: intertidal invertebrates from central California to Oregon. J. Carlton (ed.). University of California Press, Berkeley, CA.
5. CASTILLO, G. C., H. W. LI, and P. A. ROSSIGNOL. 2000. Absence of overall feedback in a benthic estuarine community: a system potentially buffered from impacts of biological invasions. *Estuaries*. 23:275-291.
6. FAUCHALD, K. 1977. The polychaete worms: definitions and keys to the orders, families, and genera. *Natural History Museum of Los Angeles County Science Series*. 28:1-190.
7. FAUCHALD, K., and P. A. JUMARS. 1979. Diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology*. 17:193-284.
8. GALLAGHER, E. D. 1979. Soft-bottom benthic succession: the "boom and crash" of an opportunist. Abstract.
9. GALLAGHER, E. D., P. A. JUMARS, and D. D. TRUEBLOOD. 1983. Facilitation of soft-bottom benthic succession by tube builders. *Ecology*. 64:1200-1216.
10. HARTMAN, O. 1951. The Littoral marine annelids of the Gulf of Mexico. Allan Hancock Foundation, University of Southern California, California.
11. —. 1969. Atlas of the Sedentariate Polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
12. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
13. OLSON, M. A., R. N. ZAJAC, and M. A. RUSSELLO. 2009. Estuarine-scale genetic variation in the polychaete *Hobsonia florida* (Ampharetidae; Annelida) in Long Island Sound and relationships to Pleistocene glaciations. *Biological Bulletin*. 217:86-94.
14. PETTIBONE, M. H. 1953. A new species of polychaete worm of the family Ampharetidae from Massachusetts. *Journal of the Washington Academy of Sciences*. 43:384-386.
15. SELF, R. F. L., and P. A. JUMARS. 1978. New resource axes for deposit feeders. *Journal of Marine Research*. 36:627-641.
16. ZOTTOLI, R. A. 1974. Reproduction and larval development of the Ampharetid Polychaete *Amphicteis floridus*. *Transactions of the American Microscopical Society*. 93:78-89.

Updated 2014

Pista pacifica

Phylum: Annelida
Class: Polychaeta
Order: Terebellida
Family: Terebellidae

Description

Size: Individuals are large reaching up to 37 cm in length and 5–6 mm in width (Hartman 1969) and inhabit tubes that can reach lengths of 1 m (Winnick 1981).

Color: Anterior segments light red to brownish pink with 12 tongue-shaped maroon lobes (Fig. 2). “Scutes” (or ventral pads) on the first segments and ventral surface gray with ochre and light yellow spots. Posterior pink and blackish, dark red branchiae and white tentacles with light gray and brown stripes.

General Morphology: These relatively large polychaetes are generally recognized by the morphology of their tube. The characteristic hood-like tube anterior extends above the sediment surface (Hartman 1969; see Kozloff 1993 plate 325).

Body: Worm is soft and fragile, particularly the feeding tentacles. Thoracic and abdominal regions are distinct with largest segments medial (Fig. 1). Body can be divided into two regions based on associated parapodia: anterior region with biramous parapodia and a posterior region with only neuropodia (family Terebellidae, Fauchald 1977).

Anterior: Prostomium is rounded and peristomium with hood-like membrane bearing tentacles (Hartman 1969) (Fig. 2). Segments 1–4 with ventrolateral lappets, which are most conspicuous on segments three and four (Hartman 1969).

Trunk: Thorax with 17 setigers (16 uncinigers) and biramous parapodia.

Tongue-shaped pads or lobes, called scutes, are present through setiger 10 (Fig. 2). Lateral lappets present on second and third branchial segments (Hartman 1969; Hilbig 2000). Abdomen with about 300 segments, bearing reduced neuropodia only and no notopodia (family Terebellidae,

Fauchald 1977). Prominent ventral groove present abdominally (Fig. 2).

Posterior: Posterior gradually tapers to a broad and flattened pygidium (Fig. 2).

Parapodia: Biramous. Notopodia bear capillary notosetae that are long, slender and limbate (= winglike) (Fig. 2). Zipper-like thoracic neuropodia contain uncini (Fig. 3), which are avicular (= beak-like) on first few segments and become short-stemmed posteriorly.

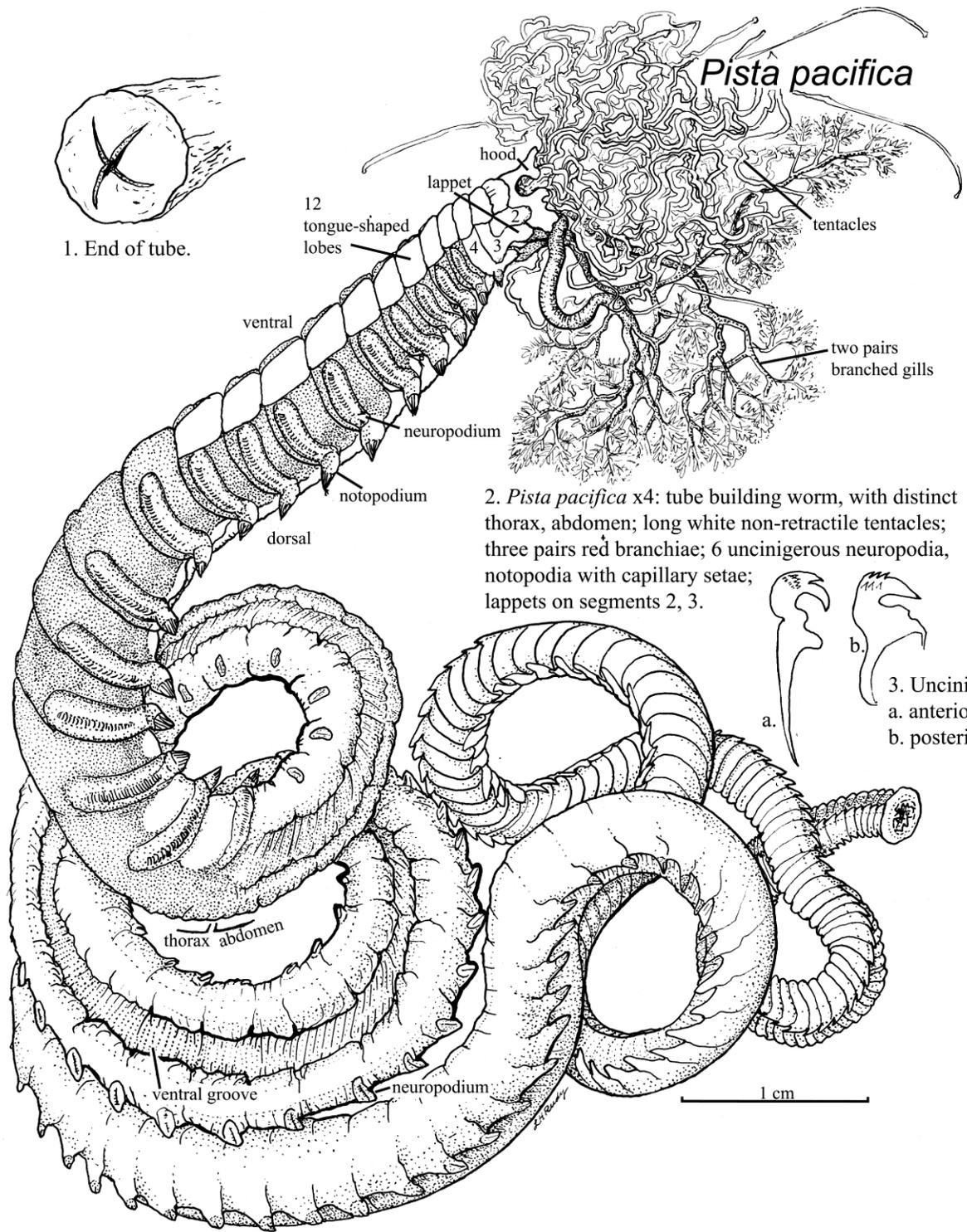
Setae (chaetae): Setae begin on segment four and consist of small fascicles arising from branchial bases. Capillary notosetae begin at segment four (Hartman 1969). Six single-row uncinigerous neurosetae begin at segment five where the first few are long-handled and avicular (Hartman 1969; Hilbig 2000) and the rest are short (Blake and Ruff 2007) (Fig. 3). The remaining 10 uncinigerous neurosetae are double-row (Hartman 1969). Abdominal uncini are avicular (Hartman 1969).

Eyes/Eyespots: None.

Anterior Appendages: Feeding tentacles are long (Fig. 2), filamentous, mucus covered and white with light stripes.

Branchiae: Three pairs of dark, red, branched gills, which are plumose and arise dorsally from segments two, three and four (Hartman 1969; Hilbig 2000) (Fig. 2). Branchiae contain vascular hemoglobin, which transfers oxygen to coelomic hemoglobin (Terwilliger 1974).

Burrow/Tube: Sand covered tube is cylindrical and consists of a rough, large anterior with overlapping membrane (often broken when animal is collected). Posterior end of tube with characteristic “star of *Pista*” pattern (Fig. 1) (Terwilliger 1974). The worm inhabits the vertical tube, which extends several centimeters above the surface sediment (Abbott and Reish 1980; Winnick 1981). The orientation of the tube has been



Pista pacifica

1. End of tube.

2. *Pista pacifica* x4: tube building worm, with distinct thorax, abdomen; long white non-retractile tentacles; three pairs red branchiae; 6 uncinigerous neuropodia, notopodia with capillary setae; lappets on segments 2, 3.

3. Uncini:
a. anterior
b. posterior.

shown to correspond to the predominant current direction (90° orientation, Winnick 1981).

Pharynx:

Genitalia:

Nephridia: The nephromixia (organs for reproduction and secretion) of the Amphitritinae and, specifically, the genus *Pista* have been described in detail (Smith 1992). *Pista pacifica* is unique within this genus in having two pairs of excretory and three pairs of reproductive nephromixia. The reproductive nephromixia are joined on each side of the body by a common duct (Smith 1992).

Possible Misidentifications

The Terebellidae are one of a number of tube-building polychaete families with soft tentacles for deposit feeding and with gills on their anterior segments (Blake and Ruff 2007). Many terebellids occur in our Northwest bays. All of them have bodies with numerous segments and two distinct regions, a tapering abdomen with neurosetae only and both capillary setae and uncinigerous tori on the thorax. They all have a modified and reduced head with the prostomium and peristomium at least partly fused and many non-retractible filiform tentacles emerging from the folded prostomium. Terebellids are relatively large, usually over 5 cm in length, and have feeding tentacles (“spaghetti worms”), which are not completely retractile into the worm’s mouth. Their branchiae are not simple, but consist of masses of aborescent or filamentous structures. There are 14 local terebellid genera (Blake and Ruff 2007): *Amaeana*, *Eupolymnia*, *Lanice*, *Loimia*, *Nicolea*, *Neoamphitrite*, *Neoleprea*, *Polycirrus*, *Proclea*, *Ramex*, *Spinospaera*, *Streblosoma*, *Thelepus* and *Pista*.

Within the genus *Pista*, there are three local species. The species with most similar morphology to *P. pacifica* is *P. elongata*. The latter species, however, has lappets on the second segment, but not on the third (as in *P. pacifica*). *Pista elongata* can further be differentiated from *P. pacifica* as the former species has no tongue-shaped lobes on the fourth segment and its tube has

a sponge-like, reticulated top (Blake and Ruff 2007). Furthermore, the tubes of *P. elongata* are in crevices among rocks, not in estuarine mud. *Pista agassizi* (= *P. brevibranchia*) is only known from California, where habitat is unknown (Blake and Ruff 2007). *Pista agassizi* has two pairs of branchiae (rather than three in *P. pacifica*), lateral lappets on segments 1–3 transitioning to smaller lobes on segments 4–6 and there is no indication of the ventral pads or scutes, which are present in *P. pacifica* (Blake and Ruff 2007). *Pista cristata* and *P. fasciata* are not currently reported between central California and Oregon (Blake and Ruff 2007). *Pista cristata*, from Puget Sound, has gills, which form a globular mass, and reaches lengths up to 9 cm. *P. fasciata*, also from Puget Sound, has prominent prostomial lobes.

Ecological Information

Range: Type locality is Vancouver Island, Canada (Hartman 1969). Range includes California to western Canada.

Local Distribution: Coos Bay sites include South Slough and Cape Arago Coves.

Habitat: Deep mud, sandy estuaries and protected bays (Abbott and Reish 1980), where it makes large tubes and is commonly found in areas of dense eel grass (Porch 1970).

Salinity:

Temperature:

Tidal Level: +0.15 m to subtidal.

Associates: The polynoid worm, *Halosydna brevisetosa*, inhabits the tube of *Pista pacifica* (Abbott and Reish 1980), in a commensal association. Other associates include white “nodding heads”, or entroprocts, which are found on worm midsection.

Abundance: 3.5/m² in eelgrass areas of South Slough (Winnick 1981).

Life-History Information

Reproduction: Terebellid reproductive and developmental modes are highly variable. Among local species, *Eupolymnia heterobranchia* (= *crescentis*), *Neoamphitrite robusta*, *Lanice conchilega* and *Amaeana occidentalis* are free spawners, with lecithotrophic larvae of short pelagic duration (seven days). *Ramex californiensis* and

Thelepus crispus brood their larvae within their tubes (Blake 1991; McHugh 1993). Little is known about the development of *Pista pacifica*, and although self-fertilization has not been confirmed for any terebellid, hermaphroditic *P. pacifica* individuals have been observed (McHugh 1993).

Larva: The only unifying feature among terebellid larvae is that they are all non-feeding (McHugh 1993). Immediately following metamorphosis (aulophore stage), two local species are known to feed in the plankton, *Lanice conchilega* and *Liomia medusa* (McHugh 1993), but they are non-feeding in their first larval stage. The development of *P. pacifica* is not known. The only locally known terebellid larvae are those of *Lanice conchilega* and *Amphitrite cirrata* (Crumrine 2001).

Juvenile:

Longevity:

Growth Rate:

Food: Detritus, picked up by thread-like tentacles and passed to mouth by cilia and mucus glands (Abbott and Reish 1980).

Predators:

Behavior:

Bibliography

1. ABBOTT, D. P., and D. J. REISH. 1980. Polychaeta: the marine annelid worms, p. 448-489. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
2. BLAKE, J. A. 1991. Larval development of Polychaeta from the northern California coast V. *Ramex californiensis* Hartman (Polychaeta: Terebellidae). *Bulletin of Marine Science*. 48:448-460.
3. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon*. J.T. Carlton (ed.). University of California Press, Berkeley, CA.
4. CRUMRINE, L. 2001. Polychaeta, p. 39-77. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
5. FAUCHALD, K. 1977. The Polychaete worms: definitions and keys to the orders, families and genera. Natural History Museum of Los Angeles County, Los Angeles.
6. HARTMAN, O. 1969. Atlas of the sedentary polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, CA.
7. HILBIG, B. 2000. Family Terebellidae, p. 231-290. *In: Taxonomic atlas of the benthic fauna of the Santa Maria Basin and western Santa Barbara Channel*. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
8. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
9. MCHUGH, D. 1993. A comparative study of reproduction and development in the polychaete family Terebellidae. *The Biological Bulletin*. 185:153-167.
10. PORCH, L. L. 1970. Polychaetes of Coos Bay. *In: OIMB Unpublished Student Report, Summer 1970*.
11. SMITH, R. I. 1992. Three nephromixial patterns in polychaete species currently assigned to the genus *Pista* (Annelida, Terebellidae). *Journal of Morphology*. 213:365-393.
12. TERWILLIGER, R. C. 1974. Oxygen equilibria of the vascular and coelomic hemoglobins of the terebellid polychaete, *Pista pacifica*: evidence for an oxygen transfer system. *Comparative Biochemistry and Physiology* 48A:745-755.
13. WINNICK, K. B. 1981. Tube hood orientations of *Pista pacifica* (Polychaeta: Terebellidae). M.S. University of Oregon.

Updated 2014

Thelepus crispus

A terebellid worm

Phylum: Annelida
Class: Polychaeta
Order: Terebellida
Family: Terebellidae

Description

Size: Individuals range in size from 70–280 mm in length (Hartman 1969). The greatest body width at segments 10–16 is 13 mm (88–147 segments). The dissected individual on which this description is based was 120 mm in length (from Coos Bay, Fig. 1).

Color: Pinkish orange and cream with bright red branchiae, dark pink prostomium and gray tentacles and peristomium.

General Morphology: Worm rather stout and cigar-shaped.

Body: Two distinct body regions consisting of a broad thorax with neuro- and notopodia and a tapering abdomen with only neuropodia.

Anterior: Prostomium reduced, with ample dorsal flap transversely corrugated dorsally (Fig. 5). Peristomium with circlet of strongly grooved, unbranched tentacles (Fig. 5), which cannot be retracted fully (as in Ampharctidae).

Trunk: Thorax with well over 25 segments (Hartman and Reish 1950). Anterior thorax not greatly enlarged. Thoracic ventral plates not clearly distinguishable (as in *Pista*) and do not extend into lappets.

Posterior:

Parapodia: Thoracic segments biramous and abdominal segments bear only neuropodia. Parapodial tori (a ridge-like parapodial branch) are longest on setigers 9–21 and become papillar posteriorly (Hartman 1969).

Setae (chaetae): Notosetae appear as groups of long capillary setae in raised parapodia (Figs. 1, 5). Each seta is limbate (wing-shaped) with smooth margins (Fig. 2) (Hartman 1969).

Notosetae present from second branchial segment (third body segment) and continue almost to the worm posterior (to 14th segment from end in mature specimens) (Hutchings and Glasby 1986). All neurosetae short handled, avicular (bird-like) uncini, imbedded in a single row on oval-shaped tori (Figs. 3, 5)

where the single row curves into a hook, then a ring in latter segments (Fig. 3). Each uncinus bears a thick, short fang surmounted by 4–5 small teeth (Hartman 1969) (two in this specimen) (Fig. 4). Uncini begin on the fifth body segment (third setiger), however, Johnson (1901) and Hartman (1969) have uncini beginning on setiger two.

Eyes/Eyespots: None.

Anterior Appendages: Feeding tentacles are long (Fig. 1), filamentous, white and mucus covered.

Branchiae: Branchiae present (subfamily Thelepinae) and with many slender single filaments (Fig. 1). Three filiform pairs are present on segments two, three, and four (Hartman 1969; Hutchings and Glasby 1986). Branchiae contain vascular hemoglobin (as in *Pista pacifica*), which transfers oxygen to coelomic hemoglobin (Garlick and Terwilliger 1974).

Burrow/Tube: Stiff tube of coarse sand, gravel and shells over a chitinous base is attached to shell and/or rock or within empty burrows.

Pharynx:

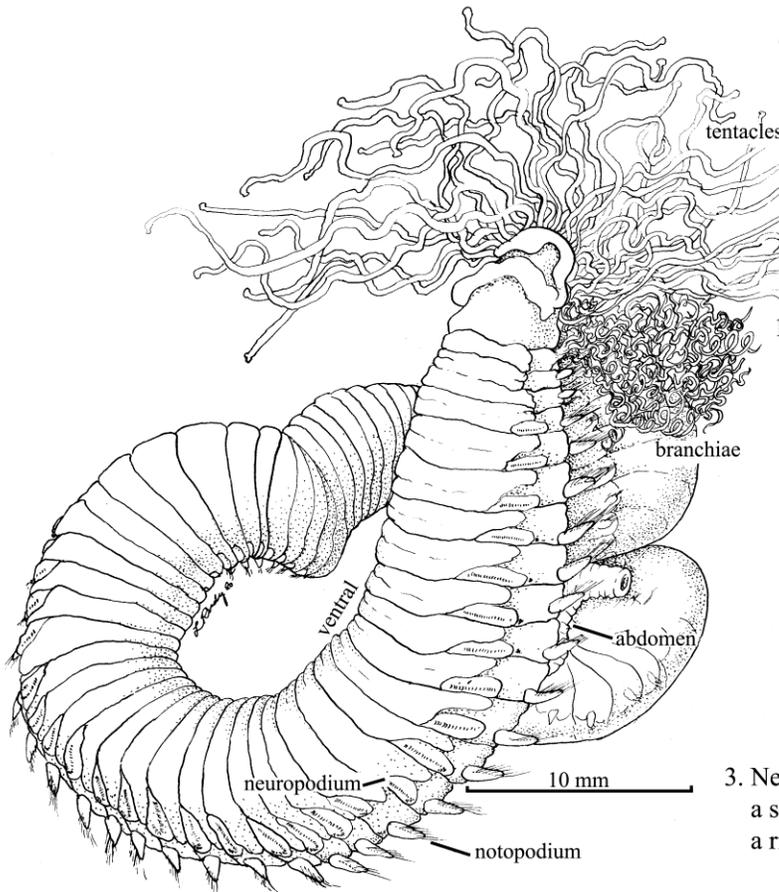
Genitalia:

Nephridia:

Possible Misidentifications

The Terebellidae are one of a number of tube-building polychaete families with soft tentacles for deposit feeding and with gills on their anterior segments (Blake 1975). Many terebellids occur in our Northwest bays. All of them have bodies with numerous segments and two distinct regions, a tapering abdomen with neurosetae only and both capillary setae and uncinigerous tori on the thorax (Berkeley and Berkeley 1952). They all have a modified and reduced head with the prostomium and peristomium at least partly fused, and many non-retractible filiform tentacles emerging from the folded prostomium. Terebellids are relatively large, usually over 5 cm in length, and have

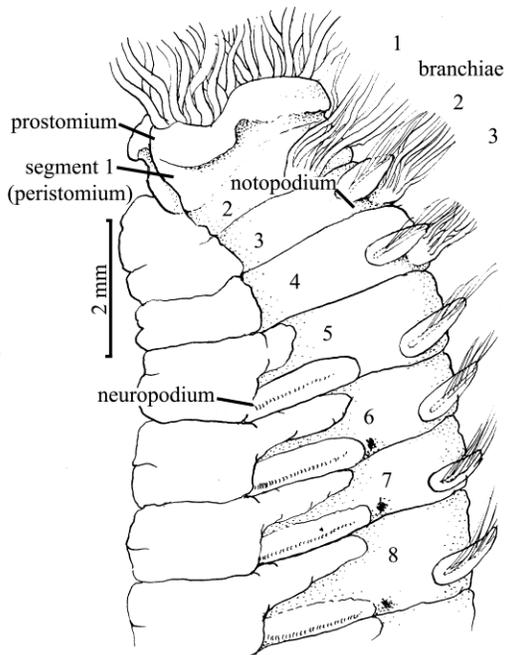
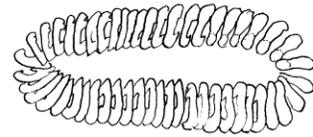
Thelepus crispus



1. *Thelepus crispus* x4:
130 segments; pinkish-orange, red
branchiae, whitish tentacles; many
thoracic segments with neuro- and
notosetae; abdomen short and with
neuropodia only .

2. A capillary notoseta:
limbate; on thoracic
setigers.

3. Neuropodial torus, medial x90:
a single row of uncini curved into
a ring, torus a low, flat oval.



4. Single uncinus:
large avicular fang
with small teeth
above it; short
handled.



5. Anterior segments x12:
branchiae - 3 pairs beginning segment 2;
capillary notosetae begin segment 3;
uncinigerous tori begin segment 5.

feeding tentacles (“spaghetti worms”) which are not completely retractile into the worm's mouth. Their branchiae are not simple, but consist of masses of aborescent or filamentous structures. There are 14 local terebellid genera (Blake and Ruff 2007): *Amaeana*, *Eupolymnia*, *Lanice*, *Loimia*, *Nicolea*, *Neoamphitrite*, *Neoleprea*, *Polycirrus*, *Proclea*, *Ramex*, *Spinosphaera*, *Streblosoma*, *Thelepus* and *Pista*.

The subfamily Thelepininae, which includes the genus *Thelepus*, always have branchiae and uncini, which occur in single rows which may curve around into a circle (e.g. Fig. 3). Other genera in this subfamily include *Streblosoma* and *Naneva* (Hartman 1969). The latter does not occur in our area. The main difference between *Streblosoma* and *Thelepus* is the position of the first notopodium and neuropodium which is the second and third segments and the third and fifth segments, for the two genera respectively (Hilbig 2000).

Streblosoma spp. have uncini arranged in single straight rows throughout the body, not changing into a depressed ring as in *Thelepus crispus*. They, too, have three pairs of branchiae and notosetae beginning on the first branchial segment, not on the second (Blake 1975). *Streblosoma* spp. can be further differentiated from *T. crispus* in that members of the former genus have many eyespots, a tightly coiled tube, a small number of tentacles and conspicuous ventral plates. *Streblosoma crassibranchia* is reported in southern and central California (Blake and Ruff 2007). *Streblosoma bairdi*, reported from Puget Sound, is small (to 80 mm), with only 30-40 setigers, a fragile posterior, notosetae beginning on the first branchial segment, and uncinial tori, which become projecting rectangular pinnules (Berkeley and Berkeley 1952; Kozloff 1974).

There are three other species of *Thelepus*, which might occur in our area. The reported range of *Thelepus hamatus* is from Alaska to California (Hilbig 2000) with a distribution that is probably subtidal and below. This species is a small, delicate terebellid, which is about 26 mm in length, with only a few thick, deeply grooved tentacles. It has only two pairs of branchiae, with few filaments and is orange. *Thelepus setosus* (= *Phenacia setosa*), a cosmopolitan

terebellid, is distinguished from *T. crispus* chiefly because all of its uncini are in single rows which do not curve into rings as in *T. crispus* and the uncini are on projecting rectangular pinnules as in *T. hamatus* (Berkeley and Berkeley 1952). *Thelepus setosus* has three pairs of branchiae and capillaries beginning on the third segment as in *T. crispus*. *Thelepus setosus* also has conspicuous black eyespots behind the tentacle bases, noticeable ventral plates (about 20) and a long narrow posterior. It is yellow to brown, with red branchiae and orange-brown tentacles (Berkeley and Berkeley 1952).

Ecological Information

Range: Type locality is San Francisco, California (Hartman 1969). Distribution along the NE Pacific from Alaska south to California.

Local Distribution: Oregon sites include Yaquina Bay (Hartman and Reish 1950). Coos Bay sites include Pigeon Point and many stations inside and outside the bay.

Habitat: *Thelepus crispus* attaches its tube to the undersides of rocks and shells. Individuals are found in Coos Bay in empty pholad (= family Pholadidae, boring clams) burrows.

Salinity: Found at salinities of 30 in Coos Bay. Individuals encountered in lower parts of bays where salinity is not likely to be reduced.

Temperature:

Tidal Level: Intertidal.

Associates: Nearly all specimens, from Coos Bay, had the polynoid polychaete, *Halosydna brevisetosa* in their burrows. In under-rock and mudflat habitats of bays, associates include *Cancer oregonensis* and burrowing clams from the genera *Adula* and *Penitella*.

Abundance: This species can be fairly abundant within its narrow habitat and is one of the most common local intertidal terebellids.

Life-History Information

Reproduction: Terebellid reproductive and developmental modes are highly variable. *Thelepus crispus* is an iteroparous brooder where individuals are continually reproductive over six months (July–December, 14°C, San Juan Island, WA, McHugh 1993). Females

spawn large (400 µm) yellow-orange oocytes (Fernald et al. 1987), which are attached in egg masses to the sides of maternal tubes in extremely large numbers (as many as 51,500 larvae per brood, McHugh 1993).

Larva: Larval developmental stages of *Thelepus crispus* are described in McHugh (1993). Larvae hatch from their brood at the one-setiger stage and have a prototroch, neurotroch, telotroch and two red eyes one day later. They have five setigers and long first tentacle at 12 days and are juveniles with eight setigers by day 26 (McHugh 1993).

Juvenile:

Longevity:

Growth Rate:

Food: A suspension and deposit feeder, *Thelepus crispus* traps detritus particles with its tentacles and passes food in a mucus film along tentacle grooves and into the mouth. Research suggests that *Thelepus crispus* orients its feeding tentacles in response to the predominating direction and strength of currents (Musgrove 1982).

Predators:

Behavior: *Thelepus crispus* contains and releases brominated aromatic metabolites into sediment surrounding their burrows. Concentrations of dibromobenzyl alcohol in surface sediments (to 6 cm depths) increased with proximity to burrows of *T. crispus* (Lincoln et al. 2005). These contaminated sediments can negatively impact the nearby community and reduce settlement and recruitment of other polychaetes (e.g. *Nereis vexillosa*, Woodin et al. 1993).

Bibliography

1. BERKELEY, E., and C. BERKELEY. 1952. Annelida: polychaeta sedentaria. Canadian Pacific Fauna. 9b:1-139.
2. BLAKE, J. A. 1975. Phylum Annelida: Class Polychaeta, p. 151-243. *In:* Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
3. BLAKE, J. A., and E. R. RUFF. 2007. Polychaeta, p. 309-410. *In:* Light and Smith manual: intertidal invertebrates from central California to Oregon. J.T. Carlton (ed.). University of California Press, Berkeley, CA.
4. FERNALD, R. L., C. O. HERMANS, T. C. LACALLI, W. H. WILSON, JR, and S. A. WOODIN. 1987. Phylum Annelida, Class Polychaeta, p. 138-195. *In:* Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
5. GARLICK, R. L., and R. C. TERWILLIGER. 1974. Coelomic cell hemoglobin of the terebellid polychaete, *Thelepus crispus* Johnson: structure and oxygen equilibrium. Comparative Biochemistry and Physiology. 47:543-553.
6. HARTMAN, O. 1969. Atlas of the sedentariate polychaetous annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles.
7. HARTMAN, O., and D. J. REISH. 1950. The Marine annelids of Oregon. Oregon State College, Corvallis, Oregon.
8. HILBIG, B. 2000. Family Terebellidae, p. 231-290. *In:* Taxonomic atlas of the benthic fauna of the Santa Maria Basin and western Santa Barbara Channel. J. A. Blake, B. Hilbig, and P. H. Scott (eds.). Santa Barbara Museum of Natural History, Santa Barbara, CA.
9. HUTCHINGS, P., and C. GLASBY. 1986. A Revision of the genus *Euthelepus* (Terebellidae: Thelepinae). Records of the Australian Museum. 38:105-117.
10. JOHNSON, H. P. 1901. The Polychaeta of the Puget Sound region. Proceedings of the Boston Society of Natural History. 29:381-437.
11. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
12. LINCOLN, D. E., K. T. FIELMAN, R. L. MARINELLI, and S. A. WOODIN. 2005. Bromophenol accumulation and sediment contamination by the marine

- annelids *Notomastus lobatus* and *Thelepus crispus*. *Biochemical Systematics and Ecology*. 33:559-570.
13. MCHUGH, D. 1993. A comparative study of reproduction and development in the polychaete family Terebellidae. *The Biological Bulletin*. 185:153-167.
 14. MUSGROVE, N. 1982. The feeding behavior of the terebellid polychaete *Thelepus crispus* Johnson in response to currents. *Journal of Shellfish Research*. 3:113.
 15. WOODIN, S. A., R. L. MARINELLI, and D. E. LINCOLN. 1993. Allelochemical inhibition of recruitment in a sedimentary assemblage. *Journal of Chemical Ecology*. 19:517-530.

Updated 2014

Sipuncula

Phascolosoma agassizi

Pacific peanut worm

Phylum: Annelida
Class: Phascolosomatida
Order: Phascolosomaformes
Family: Phascolosomatidae

Taxonomy: The evolutionary origins of sipunculans, recently considered a distinct phylum (Rice 2007), is controversial. Current molecular phylogenetic evidence (e.g., Staton 2003; Struck et al. 2007; Dordel et al. 2010; Kristof et al. 2011) suggests that Sipuncula be placed within the phylum Annelida, which is characterized by segmentation. Placement of the unsegmented Sipuncula and Echiura within Annelida, suggests that segmentation was secondarily lost in these groups (Struck et al. 2007; Dordel et al. 2010).

Description

Size: Up to 15 cm (extended) and commonly 5–7 cm in length (Rice 1975b). The illustrations are from a specimen (Coos Bay) 13 cm in length. Young individuals are 10–13 mm in length (extended, Fisher 1950). Juveniles can be up to 30 mm long (Gibbs 1985). The illustrated specimen weighed approximately 5.3 g (wet weight).

Color: Dark pigment blotches, dark conical papillae, particularly at posterior end but also along introvert (Plate 120, Rice 2007). The trunk was brown in the illustrated specimen and the skin was thick and rough, the introvert was pale, shiny, smooth, and with dark bands and splotches. The tentacles were light tan (Fig. 1).

Papillae: Papillae are conical glandular structures, each with hard round center on a platelet (Fig. 1a). Papillae are thickest around the posterior end and mid dorsally, near the anus.

Body: Body divided into anterior introvert and posterior trunk regions and the introvert can be retracted entirely into the trunk (Fig. 3) (Rice 2007). Body wall divided into longitudinal bands that can be noticeable on outside (Fig. 4). No true segmentation.

Introvert: The introvert resembles a neck and is slender and can be extended to be longer than trunk (Fig. 1) (Stephen 1964). It is composed of an anterior oral disc, which can be surrounded by ciliated tentacles, a mouth and nuchal organ (Fig. 2) (Rice 2007).

Along the introvert epidermis are spines or hooks.

Oral disc: The oral disc is bordered by a ridge (cephalic collar) of tentacles enclosing a dorsal nuchal gland. Inconspicuous, finger-like and not branched (Rice 1975b), the 18–24 tentacles exist in a crescent-shaped arc, enclosing a heart-shaped nuchal gland (Fig. 2).

Mouth: Inconspicuous and posterior to oral disc, with thin flange (cervical collar) just ventral to and outside the arc of tentacles (Fig. 2).

Eyes: A pair of ocelli at anterior end are internal and in an ocular tube (Fig. 4) (Hermans and Eakin 1969).

Hooks: Tiny chitinous spines on the introvert anterior are arranged in a variable number of dark, colored rings (usually 15–24 in this species) (Fig. 2). The first three rows can be small and colorless, while the last two can be incomplete (due to wear) (Fisher 1950).

Trunk: The trunk is bulbous, posteriorly pointed and can be divided into longitudinal bands (not always obvious exteriorly). When contracted, the trunk is peanut-shaped (Fig. 3).

Anus: Dorsal, and at anterior-most trunk (Rice 2007), the anus is recognizable as a light, raised area (Fig. 1). Intestinal tract is U-shaped (Fig. 4).

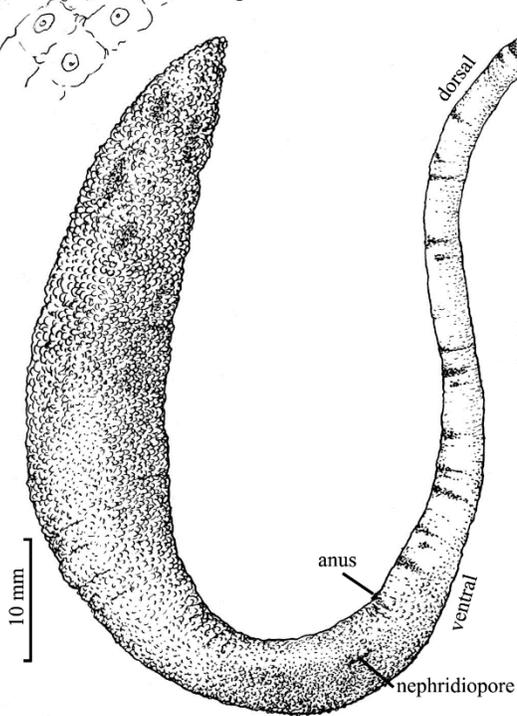
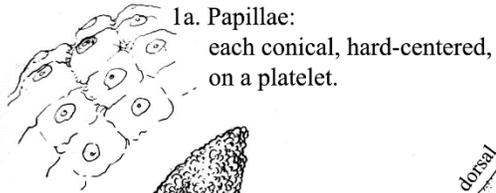
Nephridiopore: Lateral and just posterior to anus (Fig. 1). Nephridia are two long structures lying freely within the coelom (Fig. 4).

Gonads: Occur at origin of ventral retractors (Fig. 4). Sexual products (gametes) extruded through nephridiopores (Fig. 1).

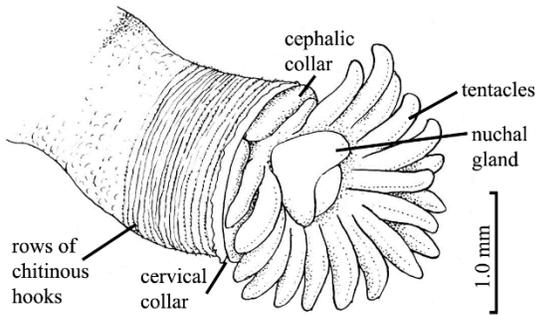
Possible Misidentifications

Sipunculans are fairly easily distinguished from other worms by their lack of segmentation and by their peanut-like shape when contracted, hence, their common name: peanut worms. The echiurans, or spoon worms, are a similar group that are also unsegmented and of a similar size,

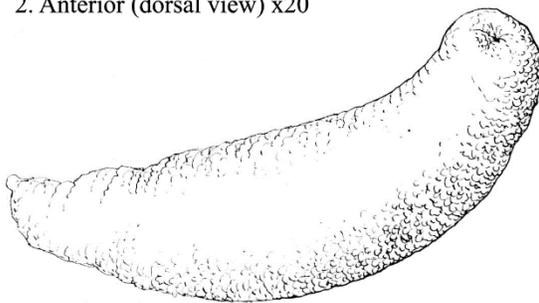
Phascolosoma agassizi



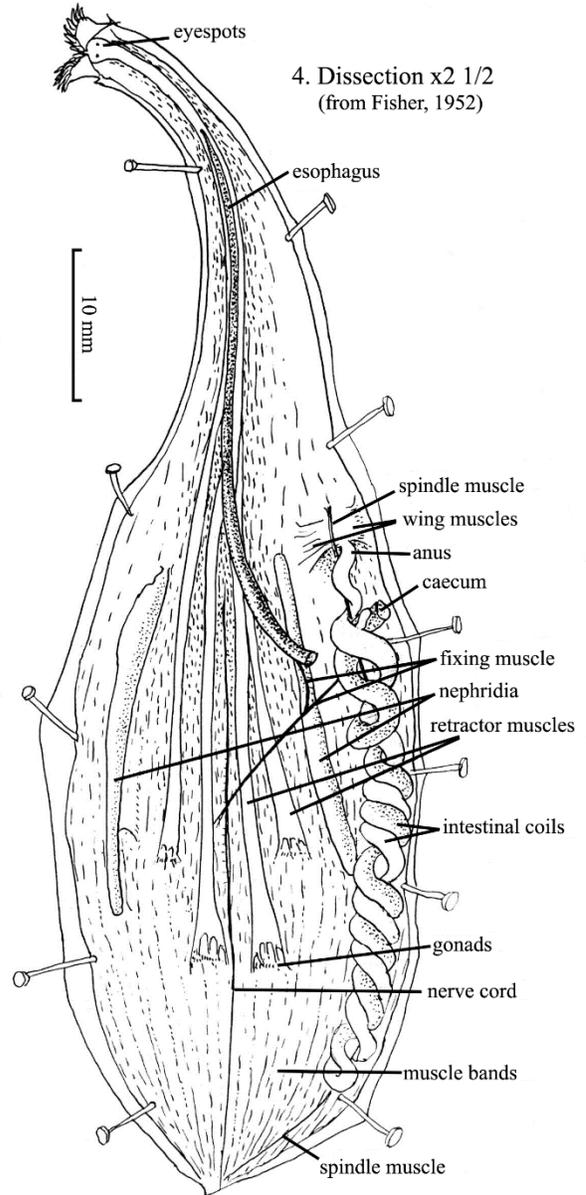
1. *Phascolosoma agassizi* x2:
peanut-shaped trunk with papillae, pigment spots;
anus dorsal, nephridiopores lateral; extrudable, pale
banded introvert with 18-24 short tentacles.



2. Anterior (dorsal view) x20



3. A contracted specimen x2



shape and habitat. They have an extensible spoon-shaped proboscis, however, and a posterior anus (not mid-body, as in Sipuncula). Priapulida is a small phylum of sausage-shaped non-segmented worms. Priapulids are predatory worms with a bulbous spiny proboscis, quite unlike any in Sipuncula. Local representatives in the Sipuncula are divided into four families: Sipunculidae, Golfingiidae, Themistidae and the Phascolosomatidae.

Phascolosoma agassizii and its family (Phascolosomatidae) are characterized by a horseshoe shaped arc of tentacles lying dorsal to the mouth by the four retractor muscles (Fig. 4) and by the longitudinal muscle bands in the body wall (except for the species *Apionsoma misakianum*, formerly *Golfingia hespera*). There are 60 species in the *Phascolosoma* genus and nearly all are distinguished by rings of single hooks on the introvert (Stephen and Edmonds 1972). Only *P. agassizii* occurs locally. *Phascolosoma japonicum*, a Japanese species, has been reported from Vancouver Island. Its trunk papillae have much larger platelets than those of *P. agassizii* (Fisher 1950). *Phascolosoma perlucens*, *P. rickettsi* (= *pectinatum*), and *P. puntarenae* are eastern Pacific species found from California southward. None of these are likely to be found in the Coos Bay area. *Phascolosoma agassizii* is readily recognizable by its long, pale introvert with dark bands and rows of hooks, its single crescent of 15–24 finger-like tentacles with the mouth outside the arc, and by its conical papillae on a rough brown trunk.

The Sipunculidae also have well defined longitudinal muscle bands in the body wall, but their oral tentacles completely surround the mouth (Stephen and Edmonds 1972; Rice 2007). Two species occur locally (*Siphonosoma ingens* and *Sipunculus nudus*) and both have a short introvert, numerous tentacles and tend to be larger than *P. agassizii* at 12–50 cm (*P. agassizii* is usually 5–7 cm) (Rice 2007).

Golfingiidae is another sipunculan family, characterized by continuous muscle tissue in the body wall (not bands). The tentacles surround the mouth (unlike the crescent shaped arc of tentacles in Phascolosomatidae). The locally occurring genus is *Golfingia*. *Golfingia (margaritacea) margaritacea*, a small and threadlike species

that is only 25 mm long. It is known (so far) only from Monterey, California (Rice 1975b). *Golfingia pugettensis* (from Puget Sound) (Fisher 1952) is whitish to dark grey, smooth, with only inconspicuous papillae. Its introvert is about half the body length, and is without hooks (Hyman 1959).

Members of the Themistidae are characterized by tentacles that are long, extending and branching (rather than filiform). Three species in the genus *Themiste* (formerly *Dendrostomum*) occur locally including *T. dyscrita*, *T. hennahi* and *T. pyroides*. *Themiste pyroides* has black or brown spines on the introvert and tentacles that form four main stems. *Themiste dyscrita* resembles *T. pyroides*, but the collar at the tentacle base is reddish purple in color. *Themiste hennahi* is similar to both species but has a cylindrical body and lacks collar pigment.

Ecological Information

Range: Type locality is Mendocino, California (Schulze et al. 2012). Known range includes Kodiak Island, Alaska, to Bay of San Quintin, Baja California. Also found in western Pacific (Adrianov et al. 2001), although see Schulze et al. (2012) for evidence that this large geographic range may include many separate and cryptic species.

Local Distribution: Coos Bay distribution includes Fossil Point, Clam Island and also on the outer coast, in the rocky intertidal at Cape Arago.

Habitat: Individuals nest or burrow in rock and gravelly mud (but without a permanent tube). Also found amongst shells, holdfasts, under rocks or in cracks with *Phyllospadix* roots and the hydrocoral, *Allopora*, in *Mytilus* beds and protected situations. Not found in shifting sediments (Fisher 1950).

Salinity: Collected at 30 in Coos Bay.

Temperature: Temperate to warm waters.

Tidal Level: From mid intertidal down to 60 m, but most common in the lower half of the intertidal zone and just below low tide (Fisher 1950).

Associates: Known associates include several polychaetes (*Thelepus* and *Glycera*), chitons, serpent stars, shore crabs, gastropod, *Nucella*.

Abundance: The most common sipunculan (California, Rice 1975b) from Alaska to Pt. Conception (Rice 1974).

Life-History Information

Reproduction: Separate sexes. Ripe individuals found with eggs January (Humboldt Bay, CA) (Fisher 1950), March–May (Monterey, CA), June–September (Puget Sound, WA) (Rice 1975a). Mature gametes can compose 37% dry mass of animal. Gametes are extruded from nephridiopores into seawater, where fertilization takes place. Of 200 specimens collected Humboldt Bay in January, all were female (Fisher 1950). Adults from Vostok Bay kept together in lab at 20–22°C spawned after several hours (Adrianov et al. 2011). Frequently, nephridiopores in males and females will be visibly swollen when ready to spawn and may spawn following collection or water changes. Spawning typically occurs at night in the lab (Rice 1987).

Embryological development is holoblastic, spiral, unequal cleavage (Sipuncula). There is data on development from the eastern and western Pacific, but the western Pacific data may be from a different species. Development is faster and eggs are smaller in *P. agassizii* from the Sea of Japan than eastern Pacific populations (Adrianov et al. 2011; Rice 1967). Eggs spherical to elliptical, 100–140 µm in diameter in Humboldt Bay, 70–100 µm in diameter in Vostok Bay, and 140 x 110 x 91 µm at their longest, widest, and thickest points in Washington (Rice 1987). Mature eggs are orange-pink (Vostok Bay), bright yellow or orange (Washington). Eggs bear a small amount of yolk and develop in the lab (18–20°C in Adrianov et al. 2011) with first cleavage, blastula, and gastrula at 2.5, 16, and 24 hrs respectively (12 °C, Rice 1987). **Larva:** *P. agassizii* has two larval stages. First, an encapsulated, non-feeding (lecithotrophic) trochophore at 2.5 days with a thick egg envelope, followed by a planktotrophic pelagosphera, with the addition of a metatrochal band of locomotory cilia at terminal end of larva (Rice 1987; see Fig. 1, 2 in Johnson 2001; Fig. 19.1–19.11 in Jaeckle and Rice 2002). Larvae feed at 8–10 days (Rice 1987), can be teleplanic and develop for up to several months in the plankton (Rice 1980), however, in culture, larvae form attachment with dish soon after beginning to feed (9–10 days, Rice 1987). Some larvae were kept up to seven months, grew to 1 mm,

but did not metamorphose into benthic juveniles (Rice 1967; Adrianov et al 2011).

Juvenile: Post-metamorphosis, juveniles have enlarged papillae, especially in the pre-anal area. Pigment includes transverse bands on the introvert, but trunk pigment spots are rare. Introvert hooks include 12–25 rings (usually 15–16). 11–12 oral disc tentacles and a single nuchal organ are present (Fisher 1950).

Longevity: Sipunculans are estimated to live for up to 25 years (Rice 1980).

Growth Rate:

Food: Individuals digest organic matter from large quantities of substrate. They can also ingest small particles by the ciliary action and mucus secretion of their tentacles.

Predators: Fish, gastropods. Humans, in tropical Indo-Pacific, utilize this species for food (Rice 1980).

Behavior: *P. agassizii* individuals are mostly sedentary and nestle or burrow into sediment by elongating and contracting their bodies. They are also commonly found in cracks or under rocks while their introvert searches actively for food.

Bibliography

1. ADRIANOV, A. V., and A. S. MAIOROVA. 2010. Reproduction and development of common species of peanut worms (Sipuncula) from the Sea of Japan. *Russian Journal of Marine Biology*. 36:1-15.
2. ADRIANOV, A. V., A. S. MAIOROVA, and V. V. MALAKHOV. 2011. Embryonic and larval development of the peanut worm *Phascolosoma agassizii* (Keferstein 1867) from the Sea of Japan (Sipuncula: Phascolosomatidea). *Invertebrate Reproduction & Development*. 55:22-29.
3. DORDEL, J., F. FISSE, G. PURSCHKE, and T. H. STRUCK. 2010. Phylogenetic position of Sipuncula derived from multi-gene and phylogenomic data and its implication for the evolution of segmentation. *Journal of Zoological Systematics and Evolutionary Research*. 48:197-207.

4. FISHER, W. K. 1950. The sipunculid genus *Phascolosoma*. *Journal of Natural History*. Series 12. 3:547-552.
5. —. 1952. The Sipunculid worms of California and Baja California. *Proceedings of the United States National Museum*. 102:371-450.
6. HERMANS, C. O., and R. M. EAKIN. 1969. Fine structure of the cerebral ocelli of a sipunculid, *Phascolosoma agassizii*. *Zellforsch Zeitschrift fur Zellforschung und Mikroskopische Anatomie*. 100:325-339.
7. HYMAN, L. H. 1959. *The Invertebrates: smaller coelomate groups*. McGraw-Hill, New York.
8. JAECKLE, W. B., and M. E. RICE. 2002. Phylum Sipuncula, p. 375-396. *In: Atlas of marine invertebrate larvae*. C. M. Young, M. A. Sewell, and M. E. Rice (eds.). Academic Press, San Diego, CA.
9. JOHNSON, K. B. 2001. Sipuncula, p. 78-82. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
10. KRISTOF, A., T. WOLLESEN, A. S. MAIOROVA, and A. WANNINGER. 2011. Cellular and muscular growth patterns during sipunculan development. *Journal of Experimental Zoology, Part B-Molecular and Developmental Evolution*. 316B:227-240.
11. RICE, M. E. 1967. A comparative study of the development of *Phascolosoma agassizii*, *Golfingia pugettensis*, and *Themiste pyoides* with a discussion of development patterns in the Sipuncula. *Ophelia*. 4:143-171.
12. —. 1974. Gametogenesis in three species of Sipuncula: *Phascolosoma agassizii*, *Golfingia pugettensis*, and *Themiste pyoides*. *La Cellule*. 70:295-313.
13. —. 1975a. Sipuncula, p. 66-127. *In: Reproduction of marine invertebrates*. Vol. 2, Entoprocts and lesser coelomates. A. C. Giese and J. S. Pearse (eds.). Academic Press, New York; London.
14. —. 1975b. Un-segmented coelomate worms, p. 128-132. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley, CA.
15. —. 1980. Sipuncula and Echiura, p. 490-498. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
16. —. 1987. Phylum Sipuncula, p. 196-204. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
17. —. 2007. Sipuncula and Echiura, p. 288-292. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
18. SCHULZE, A., A. MAIOROVA, L. E. TIMM, and M. E. RICE. 2012. Sipunculan larvae and "cosmopolitan" species. *Integrative and Comparative Biology*. 52:497-510.
19. STATON, J. L. 2003. Phylogenetic analysis of the mitochondrial cytochrome c oxidase subunit 1 gene from 13 sipunculan genera: intra- and interphylum relationships. *Invertebrate Biology*. 122:252-264.
20. STEPHEN, A. C. 1964. A revision of the classification of the Phylum Sipuncula. *Journal of Natural History Series* 13. 7:457-462.
21. STEPHEN, A. C., and S. J. EDMONDS. 1972. *The Phyla Sipuncula and Echiura*. British Museum (Natural History), London.
22. STRUCK, T. H., N. SCHULT, T. KUSEN, E. HICKMAN, C. BLEIDORN, D. MCHUGH, and K. M. HALANYCH. 2007. Annelid phylogeny and the status of Sipuncula and Echiura. *BMC Evolutionary Biology*. 7.

Updated in 2015
T.C. Hiebert and M. Jarvis

Arthropoda

Ampithoe lacertosa

A gammarid amphipod

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Amphipoda, Gammaridea
Family: Ampithoidae

Taxonomy: Known synonyms for *A. lacertosa* include *A. japonica*, *A. macrurus*, *A. scitulus*, *A. stimpsoni* and *Dexamine stitulus* (Conlan and Bousfield 1982), but only *A. lacertosa* is found in current literature.

Description

Size: Locally, individuals are 12.5–15 mm in length (South Slough of Coos Bay) (Heller 1968) and reported to 24 mm in length (Chapman 2007).

Color: Pale green to reddish brown (Straude 1987) with large red eyes and small, densely arranged, diffuse black spots. Individuals tend to have a similar color to the dominant algae in which they nest (Chapman 2007).

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) or cephalothorax includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six pairs of pleopods. The first three sets of pleopods are generally used for swimming, while the last three are simpler and surround the telson at the animal posterior. Ampithoid amphipods are in the suborder gammaridea, one of the largest groups of amphipods in marine and estuarine habitats. They have smooth bodies that are only slightly compressed (Conlan and Bousfield 1982). Keys to the Ampithoidae generally refer to male specimens, although sexual dimorphism may be weaker in this group than others (Chapman 2007).

Cephalon:

Rostrum: Lateral lobes present.

Eyes: Eyes oval and red.

Antenna 1: Flagellum of the first antenna, with 42 articles, is twice as long as that of second antenna (Fig. 1) (48–52, Barnard 1954). Total length is about as long as body (Barnard 1954). No accessory flagellum is present.

Antenna 2: Flagellum of the second antenna is with 16 articles (30, Barnard 1954) (Fig. 1).

Mouthparts: Lower lip has a gap between the sub-lobes of its outer lobes (Fig. 2).

Pereon:

Coxae:

Gnathopod 1: Male gnathopod with article five equal to or smaller than article six and palm angle oblique (Fig. 5). Female gnathopod with article five longer than six in mature, large females but can be shorter in younger ones. Female gnathopod palms are oblique (Fig. 6) (Barnard 1965).

Gnathopod 2: Mature males with transverse, sinuous palm (Fig. 4) and females with oblique palm (Fig. 6).

Pereopods 3 through 7:

Pleon:

Pleonites:

Urosomites: The first uropod is without an interramal tooth (Fig. 1b). Uropod three is with flat, setose inner ramus and two curved hooks on the outer ramus (Fig. 7).

Epimera: Two and three with small point at posterior corner (Fig. 1a).

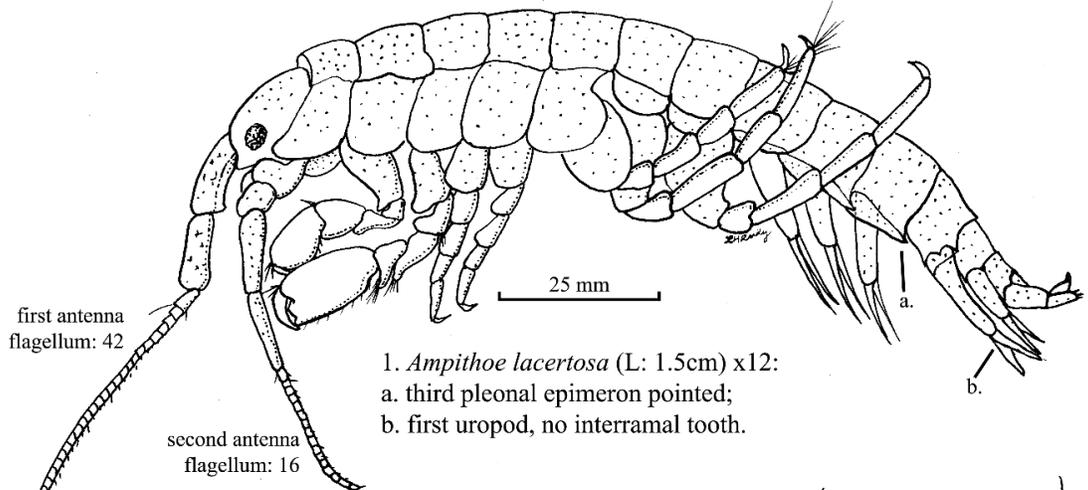
Telson: Fleshy, uncleft, rounded with two small spines laterally (Fig. 7).

Sexual Dimorphism: Among amphipods, males generally have larger eyes, antennae and gnathopods (Straude 1987). Sexual dimorphism in *A. lacertosa* is pronounced in the **gnathopods**.

Possible Misidentifications

The Ampithoidae are a family of gammarid amphipods characterized by short third uropods and rami that possess 1–2 distinctive and stout hooks on the outer ramus (Myers and Lowry 2003). They are usually sexually dimorphic and males are easier to identify than females. They are herbivorous and live in nests they create amongst algal blades or within algae stipes. There are 10–11 local species in the genus *Ampithoe* (*A. corallina* is currently a questionable species, Chapman 2007),

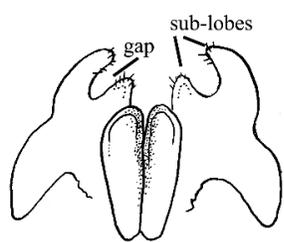
Ampithoe lacertosa



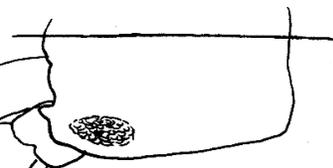
1. *Ampithoe lacertosa* (L: 1.5cm) x12:
 a. third pleonal epimeron pointed;
 b. first uropod, no interramal tooth.

first antenna
 flagellum: 42

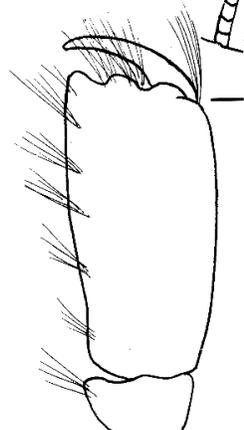
second antenna
 flagellum: 16



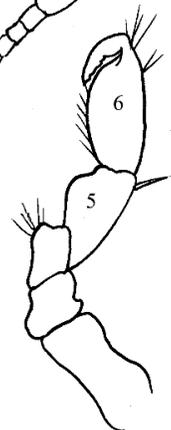
2. Lower lip:
 gap between
 sub-lobes of
 outer lobes.



3. Head and antennae:
 no accessory flagellum.



4. Second gnathopod ♂ x32:
 palm angle transverse.



5. First gnathopod ♂:
 palm angle oblique;
 length of article 5 equal to
 or less than article 6.



6. Second gnathopod
 ♀: palm angle oblique
 (and in first gnathopod ♀).

7. Telson: third uropod
 with flat, setose inner
 ramus and two curved
 hooks on outer ramus.

which are generally larger than other amphipod genera (Kozloff 1993). See Conlan and Bousfield (1982) for detailed account of *Ampithoe* characters.

Ampithoe simulans is also found in marine intertidal habitats of Coos Bay (Barnard 1965). This species has an oblique and concave article on the second gnathopod, not a transverse one. This article has a large sinus, and a small process on its inner margin (Barnard 1954). This species is primarily found on the open coast and lives within *Phyllospadix* spp. and other types of algae (Chapman 2007). *Ampithoe plumulosa*, as its name suggests, has a very setose second antenna and the first antenna is very long. The lower lips gape and are not compressed as they are in *A. valida*. This likely introduced species is often found in mussel beds (Chapman 2007). *Ampithoe pollex* does have compressed lower lips and its name comes from its large pointed process or thumb which meets the dactyl (the sixth article of the second gnathopod in males). *Ampithoe aptos* has two enlarged lobes on the apex of the telson and the fifth article of pereopod five is less than half as long as the sixth. On the other hand, *Ampithoe sectimanus* has a telson with small knobs and the fifth article of pereopod five is more than half as long as the sixth. *Ampithoe dalli* has plumose setae on the anterior edge of the second article of gnathopod one (in males). *Ampithoe longimana* is North Atlantic species, introduced to southern California and *A. ramondi* is a cosmopolitan species that is currently not reported farther north than Point Conception, California. Neither of these species are found in current local intertidal keys (Chapman 2007).

The most similar species to *A. lacertosa* is *A. valida*, which also has the transverse palm in the second male gnathopod, but which has shorter antennae and compressed lower lips. *Ampithoe valida* is an important estuarine species, occurring in brackish waters on the alga *Enteromorpha* (E. L. Bousfield, personal communication).

Ecological Information

Range: Known range includes Japan, Alaska, Washington and south to Magdalena Bay, Baja California.

Local Distribution: Coos Bay sites include Cape Arago, North Bay, Charleston and South Slough.

Habitat: Builds tubes or nests in algae (e.g. *Macrocystis*) and in eelgrass on mudflats at South Slough (Barnard 1975; Straude 1987). *Ampithoe lacertosa* was also found as a member of a phytal (drifting seaweeds) community collected from northern Japan (Sano et al. 2003).

Salinity: Collected at salinities of 30.

Temperature:

Tidal Level: Intertidal to +0.15 m and subtidal to 11 meters deep (Chapman 2007).

Associates:

Abundance:

Life-History Information

Reproduction: Most amphipods have separate sexes with some sex determination correlated with environmental conditions (Straude 1987). Females brood embryos in an external thoracic brood chamber made up of oostegites (see Fig. 11, Heller 1968) and irrigate embryos with water flow produced by pleopod movement (fifth pleopods in *A. lacertosa*). Development within this brood chamber is direct and individuals hatch as juveniles that resemble small adults, with no larval stage. Heller (1968) described many aspects of the biology of *A. lacertosa*, including the reproductive biology. Although many amphipod species exhibit an extended coupling period (e.g. *Hyale pugettensis*, Straude 1987), where males and females are physically coupled for several days prior to copulation, this is not necessary in *A. lacertosa* individuals. Instead, males and females inhabit the same nest. Fertilization occurs within the brood chamber and eggs are laid directly into brood pouch from oviducts five hours after fertilization. Eggs are surrounded by a transparent membranous sac and broods range in number from 10–155 (average 64) embryos that are elliptical in shape and approximately 450–560 μm in diameter. At 8–10°C, individuals hatch at 22 days post fertilization, but remain in the female brood pouch for another 19 days. This timeline increases at warmer temperatures (e.g. 19 and 10 days at 12–15°C) (Heller 1968; Straude 1987).

Larva: Since most amphipods are direct developing, they lack a definite larval stage. Instead, this young developmental stage

resembles small adults (e.g. Fig. 39.1, Wolff 2014).

Juvenile: Sexual maturity is reached at four months in water temperatures from 8–12°C. Female oostegites appear after the fifth molt and male genitals are apparent after the second molt. Sexual maturity is reached by the sixth or seventh molt in males and the tenth molt in females (Heller 1968).

Longevity:

Growth Rate: Amphipod growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens (Ruppert et al. 2004). Time between molts increases with age and averages 49 days in mature female *A. lacertosa* (Heller 1968).

Food: The Ampithoidae are an amphipod group, specialized for herbivorous feeding on algae (Myers and Lowry 2003). Grazing by *Ampithoe* amphipods (e.g. *A. longimana*) can have a significant impact on the structure of algal communities (Duffy and Hay 2000) and experimentally adjusting feeding diversity (rather than phylogenetic diversity) leads to a community with a larger number of species (Best et al. 2013). Grazing studies have shown that *A. lacertosa* grazes macroalgae (e.g. *Ulva* spp.) faster than eelgrasses, while the opposite is true for the grazing habits of the congener, *A. valida*, who consume eelgrasses more readily than macroalgae (Best and Stachowicz 2012). *Ampithoe lacertosa* fed on a wide variety of algae in a recent study (*Ulva lactuca*, *Mazzaella splendens*, *Alaria marginata*, *Desmarestia ligulata*, *Fucus distichus edentatus* and *Saccharina latissima*, McDonald and Bingham 2010).

Predators: The *Ampithoe* congener, *A. longimana*, is preyed upon by the pinfish, *Lagodon rhomboides*, and the grass shrimp, *Palaemonetes vulgaris* (Nelson 1979).

Behavior: A tube-dweller that builds simple, but temporary tubes (McDonald and Bingham 2010).

Bibliography

1. BARNARD, J. L. 1954. Marine amphipoda of Oregon. Oregon State Monographs, Studies in Zoology. No. 8:1-103.
2. —. 1965. Marine amphipoda of the family Ampithoidae from Southern California. Proceedings of the U.S. Natural Museum. 118:1-46.
3. —. 1975. Phylum Anthropoda: Crustacea, Amphipoda: Gammaridea, p. 313-366. *In*: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
4. BEST, R. J., N. C. CAULK, and J. J. STACHOWICZ. 2013. Trait vs. phylogenetic diversity as predictors of competition and community composition in herbivorous marine amphipods. Ecology Letters. 16:72-80.
5. BEST, R. J., and J. J. STACHOWICZ. 2012. Trophic cascades in seagrass meadows depend on mesograzers variation in feeding rates, predation susceptibility, and abundance. Marine Ecology Progress Series. 456:29-42.
6. CHAPMAN, J. W. 2007. Arthropoda: Amphipoda: Gammaridea, p. 545-618. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.).
7. CONLAN, K. E., and E. L. BOUSFIELD. 1982. The amphipod superfamily Corophioidea in the northeastern Pacific region. Family Ampithoidae: systematics and distributional ecology. Publications in Biological Oceanography National Museum of Natural Sciences Canada. 10:41-75.
8. DUFFY, J. E., and M. E. HAY. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. Ecological Monographs. 70:237-263.
9. HELLER, S. P. 1968. Some aspects of the biology and development of *Ampithoe lacertosa* (Crustacea: Amphipoda). University of Washington, Seattle, WA.
10. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.

11. MCDONALD, P. S., and B. L. BINGHAM. 2010. Comparing macroalgal food and habitat choice in sympatric, tube-building amphipods, *Ampithoe lacertosa* and *Peramphithoe humeralis*. *Marine Biology*. 157:1513-1524.
12. MYERS, A. A., and J. K. LOWRY. 2003. A phylogeny and a new classification of the Corophiidea (Leach, 1814) (Amphipoda). *Journal of Crustacean Biology*. 23:443-485.
13. NELSON, W. G. 1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *Journal of Experimental Marine Biology and Ecology*. 38:225-245.
14. RUPPERT, E.E., R.S. FOX, and R.D BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*, 7th Edition. Thomson Brooks/Cole, Belmont, CA.
15. SANO, M., M. OMORI, and K. TANIGUCHI. 2003. Predator-prey systems of drifting seaweed communities off the Tohoku coast, northern Japan, as determined by feeding habit analysis of phytal animals. *Fisheries Science*. 69:260-268.
16. STRAUDE, C. P. 1987. Phylum or Subphylum Crustacea, Class Malacostraca, order Amphipoda, p. 424-431. *In: Reproduction and development of marine onvertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
17. WOLFF, C. 2014. Amphipoda, p. 206-209. *In: Atlas of crustacean larvae*. J.W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.

Updated 2015

Ampithoe valida

A gammarid amphipod

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Amphipoda, Gammaridea
Family: Ampithoidae

Description

Size: Both illustrated specimens (from Coos Bay), a male and female, were 10 mm in length. Size range up to 12.5 mm (Chapman 2007).

Color: Green with black chromatophores and red eyes.

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) or cephalothorax includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six pairs of pleopods. The first three sets of pleopods are generally used for swimming, while the last three are simpler and surround the telson at the animal posterior. Ampithoid amphipods are in the suborder gammaridea, one of the largest groups of amphipods in marine and estuarine habitats. They have smooth bodies that are only slightly compressed (Conlan and Bousfield 1982). Keys to the Ampithoidae generally refer to male specimens, although sexual dimorphism may be weaker in this group than others (Chapman 2007).

Cephalon:

Rostrum:

Eyes:

Antenna 1: The first and second antennae are of equal length in males (Fig. 1), but the first antenna is slightly longer in females. Both first and second antennae bear a few setae, but no spines (Barnard 1965). No accessory flagellae are present.

Antenna 2:

Mouthparts: Lower lip with a notch between the sublobes and outer lobes (Fig. 5) (Ampithoidae, Barnard 1965) and sublobes are compressed. Mandible is with a large palp and an obvious rasping surface (Fig. 2).

Pereon:

Coxae: Coxa one extended anteriorly, particularly coxal plate one (Fig. 1) (Barnard 1965).

Gnathopod 1: Male gnathopod article five has a distal projection and is slightly longer than article six. Article two is very setose and article six has an oblique angle to the palm (Fig. 3). The gnathopod palm in females is also oblique (not figured).

Gnathopod 2: Male gnathopod articles two and three have large rounded lobes. Article five is with a narrow hind lobe, article six is elongate, rectangular, with a transverse palm and a quadrate middle bump and dactyl (article seven) is curved (Fig. 4). Female gnathopod two is like female gnathopod one (palm oblique), but stouter.

Pereopods 3 through 7:

Pleon:

Pleonites:

Urosomites: All three urosomites short and the first two have spines (Fig. 1). Uropod one is with a vestigial peduncular process. Third uropods are with two hooks on the stout outer ramus (Barnard 1965) and the inner ramus is flattened, with bristles (Kozloff 1974) (Fig. 6).

Epimera: The second and third epimera are rounded, with very slight points (Barnard 1965) (Fig. 1).

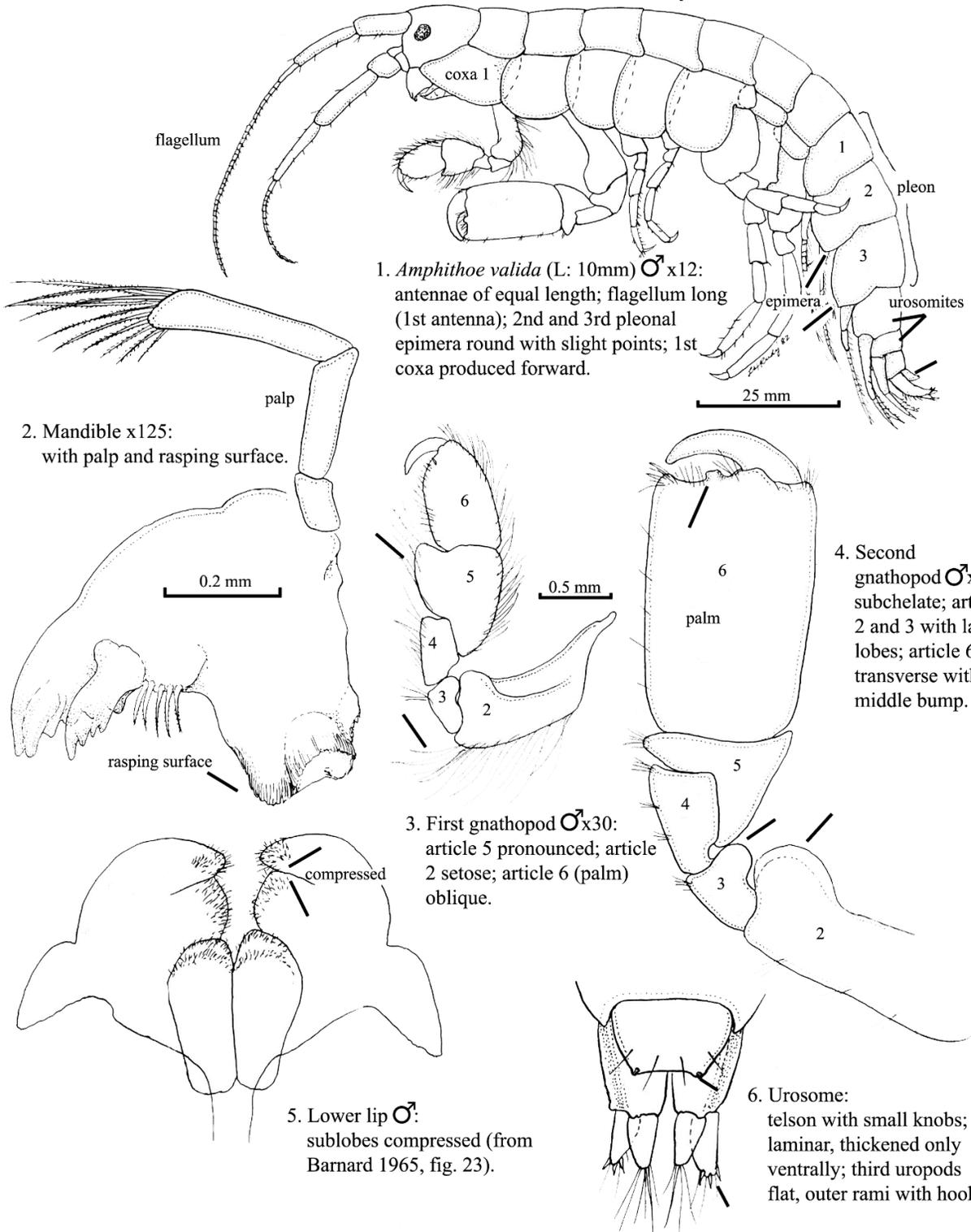
Telson: Telson is blunt and with small knobs at posterior corners (Fig. 6).

Sexual Dimorphism: Among amphipods, males generally have larger eyes, antennae and gnathopods (Straude 1987). Sexual dimorphism in *A. valida* is pronounced in the **antennae** and **gnathopods**, particularly the second gnathopods (Alonso et al. 1995), and species determination must be made from male specimen.

Possible Misidentifications

The Ampithoidae are a family of gammarid amphipods characterized by short third uropods and rami that possess 1–2 distinctive and stout hooks on the outer ramus (Myers and Lowry 2003). They are usually sexually dimorphic and males are

Amphithoe valida



1. *Amphithoe valida* (L: 10mm) ♂ x12: antennae of equal length; flagellum long (1st antenna); 2nd and 3rd pleonal epimera round with slight points; 1st coxa produced forward.

2. Mandible x125: with palp and rasping surface.

4. Second gnathopod ♂ x30: subchelate; articles 2 and 3 with large lobes; article 6 transverse with middle bump.

3. First gnathopod ♂ x30: article 5 pronounced; article 2 setose; article 6 (palm) oblique.

5. Lower lip ♂: sublobes compressed (from Barnard 1965, fig. 23).

6. Urosome: telson with small knobs; laminar, thickened only ventrally; third uropods flat, outer rami with hooks.

easier to identify than females. They are herbivorous and live in nests they create amongst algal blades or within algae stipes. There are 10–11 local species in the genus *Ampithoe* (*A. corallina* is currently a questionable species, Chapman 2007), which are generally larger than other amphipod genera (Kozloff 1993). See Conlan and Bousfield (1982) for detailed account of *Ampithoe* characters.

Ampithoe simulans is also found in marine intertidal habitats of Coos Bay (Barnard 1965). This species has an oblique and concave article on the second gnathopod, not a transverse one. This article has a large sinus, and a small process on its inner margin (Barnard 1954). This species is primarily found on the open coast and lives within *Phyllospadix* spp. and other types of algae (Chapman 2007).

Ampithoe plumulosa, as its name suggests, has a very setose second antenna and the first antenna is very long. The lower lips gape and are not compressed as they are in *A. valida*. This likely introduced species and is often found in mussel beds (Chapman 2007). *Ampithoe pollex* does have compressed lower lips and its name comes from its large pointed process or thumb which meets the dactyl (the sixth article of the second gnathopod in males). *Ampithoe aptos* has two enlarged lobes on the apex of the telson and the fifth article of pereopod five is less than half as long as the sixth. On the other hand, *Ampithoe sectimanus* has a telson with small knobs and the fifth article of pereopod five is more than half as long as the sixth. *Ampithoe dalli* has plumose setae on the anterior edge of the second article of gnathopod one (in males). *Ampithoe longimana* is North Atlantic species, introduced to southern California, and *A. ramondi* is a cosmopolitan species that is currently not reported farther north than Point Conception, California. Neither of these species are found in current local intertidal keys (Chapman 2007).

Ampithoe lacertosa, another common local species found in estuaries, is very similar in appearance to *A. valida*. It differs chiefly in its lower lip, which gapes. The antennae are unequal in *A. lacertosa*, the first being longer than the second. The sixth article of the second gnathopod is transverse and sinous, but

lacks the central bump present in *A. valida*. The fifth article of gnathopod one also lacks the distal projection present in *A. valida*.

Ecological Information

Range: Type locality is Long Island Sound in the North Atlantic (Alonso et al. 1995). Known Pacific range includes British Columbia to southern California and also Japan (Carlton 1979) and Korea (Alonso et al. 1995). Range on Atlantic coast extends from New Hampshire to Chesapeake Bay (Carlton 1979). This species is native to the Atlantic coast and was introduced to the western coast (Chapman 2007). The range of this species was recently extended as far south as Quequen and Chubut Argentina (Alonso et al. 1995). Recent genetic analysis of northeast Pacific *A. valida* populations suggests three distinct lineages that may represent three cryptic species. Furthermore, these lineages suggest three separate introductions to the western coast of the United States (see Figs. 4–5, Pilgrim and Darling 2010).

Local Distribution: Coos Bay sites in South Slough (Barnard 1954), especially in the Metcalf Preserve.

Habitat: Tube dweller amongst eelgrass (Barnard 1975) and green and red algae (Alonso et al. 1995), especially *Enteromorpha* and *Ulva* spp. habitats. (This specimen built a tube in lab petri dish.) *Ampithoe valida* is a biofouling organism, and is often found on floats, pilings and docks (Chapman 2007; Pilgrim and Darling 2010).

Salinity: Collected at salinities as low as 5 and occurs in brackish waters.

Temperature:

Tidal Level: Collected at + 0.15 m MLLW and found subtidally at depths up to 30 m (Chapman 2007).

Associates: Associates in South Slough include the introduced corophiid amphipod, *Grandidierella japonica*, and the sacoglossan, *Aplysiopsis enteromorphae* (= *smithi*).

Abundance: Locally common and abundant in South Slough. In Argentina, abundance of *A. valida* was highest in the summer months with 727 individuals per 0.125 square meter (Alonso et al. 1995). In Portugal, *A. valida* densities showed a direct and positive correlation with areas of nutrient enrichment, where abundances were up to 2026

individuals per square meter in areas of high eutrophication (Pardal et al. 2000).

Life-History Information

Reproduction: Most amphipods have separate sexes with some sex determination correlated with environmental conditions (Straude 1987). Females brood embryos in an external thoracic brood chamber and irrigate embryos with water flow produced by pleopod movement. Development within this brood chamber is direct and individuals hatch as juveniles that resemble small adults, with no larval stage. The embryos of *A. valida* are oval in shape, white to yellow in color, females produce 2–3 broods each year and the number of embryos per brood may (Alonso et al. 1995) or may not be (Pardal et al. 2000) positively correlated with adult female body size. Although many amphipod species exhibit an extended coupling period (e.g. *Hyale pugettensis*, Straude 1987), where males and females are physically coupled for several days prior to copulation, there is no such period in *A. valida* individuals. Instead, males and females inhabit the same nest, although males may visit the nests of many different females (“cruising males”, Borowsky 1983). Aspects of the developmental biology of *A. valida*, were described by Barrett (1966). Female broods range in number from 3–60 (average 22) eggs which are 460 µm in diameter. At 8–10°C, individuals hatch at 10 days post fertilization, but remain in the female brood pouch for another 4 days. This timeline increases at warmer temperatures (e.g. 7 and 4 days at 12–15°C) (Heller 1968; Barrett 1966). Barrett (1966) found that brood size more accurately correlates to pereon length (not total body length). Reproductive characters of the congener, *A. longimana*, include an average brood size of only nine individuals and egg size of 420 µm (Nelson 1980) and *A. lacertosa* have broods with 10–155 (average 64) embryos that are elliptical in shape and approximately 450–560 µm in diameter. At 8–10°C, individuals hatch at 22 days post fertilization, but remain in the female brood pouch for another 19 days size (Heller 1968).

Larva: Since most amphipods are direct developing, they lack a definite larval stage. Instead this young developmental stage resembles small adults (e.g. Fig. 39.1, Wolff 2014).

Juvenile: Immature females can be differentiated from mature females by the presence of a brood pouch and associated setae for securing embryos (Alonso et al. 1995). Males reach sexual maturity earlier than females (compare 24–44 days with 28–61 days, Pardal et al. 2000).

Longevity: Range from 191–242 days (Pardal et al. 2000).

Growth Rate: Amphipod growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens (Ruppert et al. 2004). *Ampithoe valida* grows at a rate of 1 mm per week to a maximum size of 18 mm (Nicotri 1980).

Food: The Ampithoidae are notable for their specialized feeding on algae (Myers and Lowry 2003). Grazing by *Ampithoe* amphipods (e.g. *A. longimana*) can have a significant impact on the structure of algal communities (Duffy and Hay 2000) and experimentally adjusting feeding diversity (rather than phylogenetic diversity) leads to a community with a larger number of species (Best et al. 2013). Grazing studies have shown that *A. lacertosa* grazes macroalgae (e.g. *Ulva* spp.) faster than eelgrasses, while the opposite is true for the grazing habits of the congener, *A. valida*, that consumes eelgrasses more readily than it does macroalgae (Best and Stachowicz 2012) where it is often found on the flowering structures of eelgrasses (Reynolds et al. 2012). However, other researchers have shown that *A. valida* prefers soft, filamentous or bladed algae including *Enteromorpha*, *Ulva*, *Ceramium*, *Gracilaria* and *Porphyra* spp (Nicotri 1980; Cruz-Rivera and Hay 2003; Zheng et al. 2013) and populations decline when no such algae is available (Grilo et al. 2009). Chemically defended algae (e.g. *Dictyota menstrualis*) are eaten by *A.*

longimana, but are avoided by *A. valida* (Duffy and Hay 1994; Kubanek et al. 2004).

Predators: The *Ampithoe* congener, *A. longimana*, is preyed upon by the pinfish, *Lagodon rhomboides*, and the grass shrimp, *Palaemonetes vulgaris* (Nelson 1979). *Ampithoe longimana* may reduce predation from these omnivores by ingesting and concentrating the toxins of the chemically defended brown alga *Dictyota menstrualis* (Duffy and Hay 1994).

Behavior: A tube-dweller that rarely leaves the tube, *A. valida* can swim rapidly for short periods if needed (Nicotri 1980).

Bibliography

1. ALONSO, G., A. TABLADO, J. LOPEZ GAPPA, and N. MAGALDI. 1995. Seasonal changes in an intertidal population of the amphipod *Ampithoe valida* (Smith, 1873). *Oebalia*. 21:77-91.
2. BARNARD, J. L. 1954. Marine amphipoda of Oregon. Oregon State Monographs, Studies in Zoology. No. 8:1-103.
3. —. 1965. Marine amphipoda of the family Ampithoidae from Southern California. *Proceedings of the U.S. Natural Museum*. 118:1-46.
4. —. 1975. Phylum Anthropoda: Crustacea, Amphipoda: Gammaridea, p. 313-366. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
5. BARRETT, B. E. 1966. A contribution to the knowledge of the amphipodous crustacean *Ampithoe valida* Smith 1873. Ph.D. University of New Hampshire.
6. BEST, R. J., N. C. CAULK, and J. J. STACHOWICZ. 2013. Trait vs. phylogenetic diversity as predictors of competition and community composition in herbivorous marine amphipods. *Ecology Letters*. 16:72-80.
7. BEST, R. J., and J. J. STACHOWICZ. 2012. Trophic cascades in seagrass meadows depend on mesograzers: variation in feeding rates, predation susceptibility, and abundance. *Marine Ecology Progress Series*. 456:29-42.
8. BOROWSKY, B. 1983. Reproductive behavior of three tube-building peracarid crustaceans: the amphipods *Jassa falcata* and *Ampithoe valida* and the tanaid *Tanais cavolinii*. *Marine Biology*. 77:257-263.
9. CARLTON, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. University of California, Davis.
10. CHAPMAN, J. W. 2007. Amphipoda: Gammaridea, p. 545-611. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
11. CONLAN, K. E., and E. L. BOUSFIELD. 1982. The Amphipod superfamily Corophioidea in the northeastern Pacific region. Family Ampithoidae: systematics and distributional ecology. *Publications in Biological Oceanography National Museum of Natural Sciences Canada*. 10:41-75.
12. CRUZ-RIVERA, E., and M. E. HAY. 2003. Prey nutritional quality interacts with chemical defenses to affect consumer feeding and fitness. *Ecological Monographs*. 73:483-506.
13. DUFFY, J. E., and M. E. HAY. 1994. Herbivore resistance to seaweed chemical defense: the roles of mobility and predation risk. *Ecology*. 75:1304-1319.
14. —. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. *Ecological Monographs*. 70:237-263.
15. GRILO, T. F., P. G. CARDOSO, M. DOLBETH, and M. A. PARDAL. 2009. Long-term changes in amphipod population dynamics in a temperate estuary following ecosystem restoration. *Hydrobiologia*. 630:91-104.
16. HELLER, S. P. 1968. Some aspects of the biology and development of *Ampithoe lacertosa* (Crustacea: Amphipoda). University of Washington, Seattle, WA.
17. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
18. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.

19. KUBANEK, J., S. E. LESTER, W. FENICAL, and M. E. HAY. 2004. Ambiguous role of phlorotannins as chemical defenses in the brown alga *Fucus vesiculosus*. *Marine Ecology Progress Series*. 277:79-93.
20. MYERS, A. A., and J. K. LOWRY. 2003. A phylogeny and a new classification of the Corophiidea (Leach, 1814) (Amphipoda). *Journal of Crustacean Biology*. 23:443-485.
21. NELSON, W. G. 1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. *Journal of Experimental Marine Biology and Ecology*. 38:225-245.
22. —. 1980. Reproductive patterns of Gammaridean amphipods. *Sarsia*. 65:61-71.
23. NICOTRI, M. E. 1980. Factors involved in herbivore food preference. *Journal of Experimental Marine Biology and Ecology*. 42:13-26.
24. PARDAL, M. A., J. C. MARQUES, I. METELO, A. I. LILLEBO, and M. R. FLINDT. 2000. Impact of eutrophication on the life cycle, population dynamics and production of *Ampithoe valida* (Amphipoda) along an estuarine spatial gradient (Mondego Estuary, Portugal). *Marine Ecology Progress Series*. 196:207-219.
25. PILGRIM, E. M., and J. A. DARLING. 2010. Genetic diversity in two introduced biofouling amphipods (*Ampithoe valida* & *Jassa marmorata*) along the Pacific North American coast: investigation into molecular identification and cryptic diversity. *Diversity and Distributions*. 16:827-839.
26. REYNOLDS, L. K., L. A. CARR, and K. E. BOYER. 2012. A non-native amphipod consumes eelgrass inflorescences in San Francisco Bay. *Marine Ecology Progress Series*. 451:107-118.
27. RUPPERT, E.E., R.S. FOX, and R.D BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*, 7th Edition. Thomson Brooks/Cole, Belmont, CA.
28. STRAUDE, C. P. 1987. Phylum or Subphylum Crustacea, Class Malacostraca, order Amphipoda, p. 424-431. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
29. WOLFF, C. 2014. Amphipoda, p. 206-209. *In: Atlas of crustacean larvae*. J.W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
30. ZHENG, X., L. HUANG, Y. LI, and R. LIN. 2013. The feeding selectivity of an herbivorous amphipod *Ampithoe valida* on three dominant macroalgal species of Yundang Lagoon. *Acta Ecologica Sinica*. 33:7166-7172.

Updated 2015

Eogammarus confervicolus

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Amphipoda, Gammaridea
Family: Anisogammaridae

Taxonomy: Originally described as *Maera confervicolus*, *E. confervicolus* has undergone various generic designations including *Gammarus* and, most recently, *Anisogammarus*. In 1979, Bousfield revised the family Anisogammaridae and promoted *Eogammarus* to generic rank comprising 10 species (including *E. confervicolus*, Tomikawa et al. 2006). Species within this genus remain difficult to identify, however, because original descriptions often lack sufficient detail.

Description

Size: Individuals up to 19 mm. Male specimens range locally from 12 mm (South Slough of Coos Bay) to 16 mm in length (Siuslaw Estuary).

Color: White with dark brown mottling and brown stripes on the first and second antennae.

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) or cephalothorax includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six pairs of pleopods. The first three sets of pleopods are generally used for swimming, while the last three are simpler and surround the telson at the animal posterior. Amphipods in the Gammaroidea (including Gammaridae and Anisogammaridae) display weak sexual dimorphism (Chapman 2007). (For detailed key and description of *E. confervicolus* see Figs. 14–17 Tomikawa et al. 2006).

Cephalon:

Rostrum: Rostrum vestigial.

Eyes:

Antenna 1: Almost equal to ½ body length and with an accessory flagellum of five articles (Fig. 1). Longer than (or equal to) second antenna and with posterodistal spine on peduncle (Fig. 1) (*Eogammarus*, Bousfield

1979). Posterodistal setae on article one spiniform (Tomikawa et al. 2006).

Antenna 2: Stout, shorter than first and with 14 articles (Fig. 1). Peduncles four and five with two (rarely three) posterior marginal groups of setae (in addition to terminal group) (Bousfield 1979; Tomikawa et al. 2006).

Mouthparts: Mandible with palp, molar large and bears rasping surface. No palp setae on the first article of maxilla one (Tomikawa et al. 2006).

Pereon:

Coxae: First four coxal plates become gradually larger and the fourth is rounded (Fig. 1) while plates 5–7 are quite small.

Gnathopod 1: Slightly smaller than second gnathopod. Article six with palm oblique, nine peg-like teeth and dactyl curved (Fig. 2a).

Gnathopod 2: Much like the first gnathopod, but larger and palm with seven stout pegs (Fig. 2b).

Pereopods 3 through 7: Strong, becoming larger posteriorly and spinous but without plumose setae on margins of basis and carpus (Tomikawa et al. 2006).

Pleon:

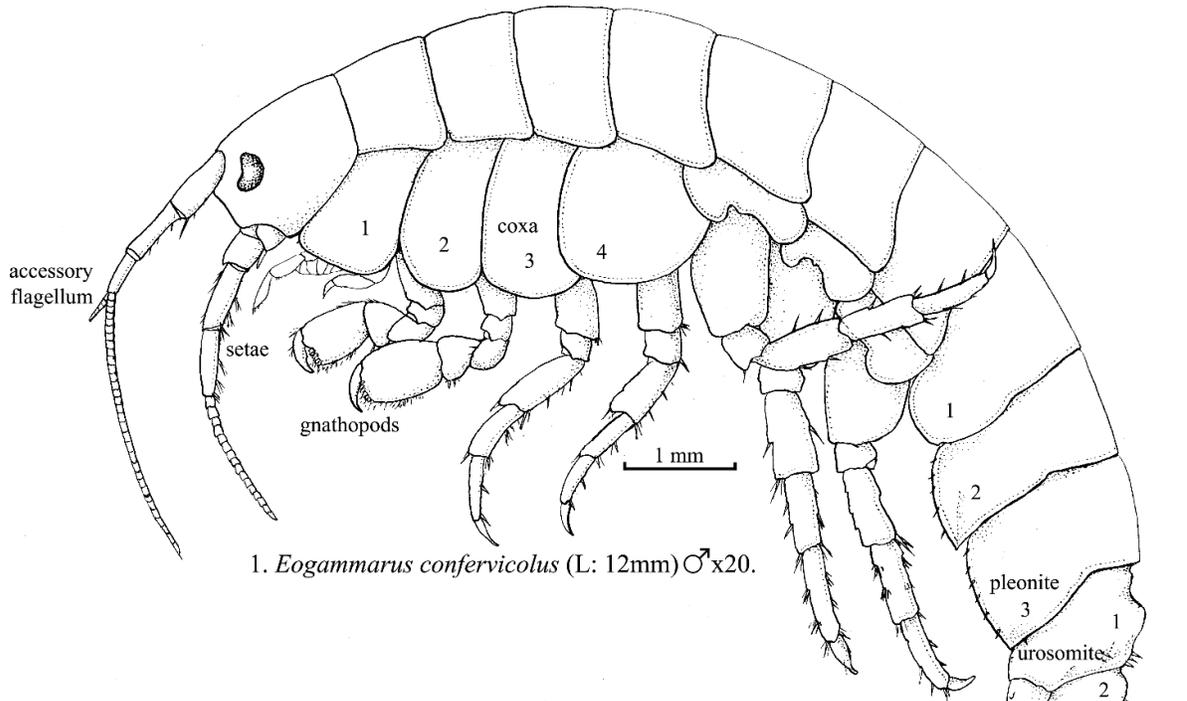
Pleonites: No dorsal spines and only 0–2 posterior marginal setae (Fig. 1).

Urosomites: Urosome one with four dorsal groups of three spines each. Urosome two with dorsal spines in two groups and no prominent median tooth (Fig. 3) (key taxonomic character, Bousfield 1979). Uropods one and two with 2–4 groups of spines. Uropod two with rami extending beyond peduncle of uropod three (Fig. 1) (Bousfield 1979). The inner margin of the outer ramus in uropod three usually with four groups of strong spines, but less than 10 isolated plumose setae. The inner ramus is less than ½ length outer ramus (Fig. 4) (Bousfield 1979).

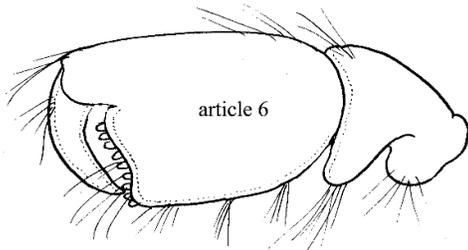
Epimera:

Telson: Split, with connected lobes each with two spines, and only one spine is apical (at

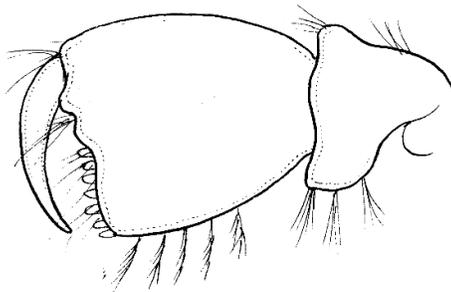
Eogammarus confervicolus



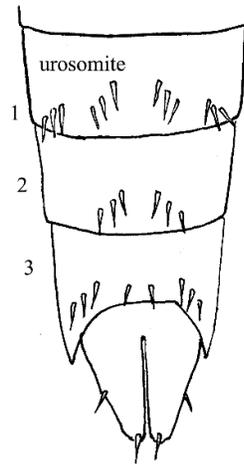
1. *Eogammarus confervicolus* (L: 12mm) ♂ x20.



2a. First gnathopod ♂:
9 pegs, strongly curved dactyl.



2b. Second gnathopod ♂:
7 pegs, 5 fascicles; narrow dactyl.



3. "Basic" gammarid split telson,
connected lobes, each with two spines;
urosomites: stout spines aligned
anterior to posterior.



4. Third uropod with
small inner branch.

the tip) (Fig. 3). *Eogammarus confervicolus* and *E. oclairi* can be differentiated by telson characters, as the latter species only has one spine on each lobe. However, it is currently unclear whether this feature is representative of two species, or if *E. oclairi* is simply large *E. confervicolus* (Bousfield 1979; Chapman 2007).

Sexual Dimorphism: Sexual dimorphism is relatively weak among the Gammaroidea compared to other amphipod families. Female and male *E. confervicolus* differ very little, if at all. Females can be smaller, have smaller **gnathopods**, and shorter **antenna** than do the males.

Possible Misidentifications

Gammaroidea comprises the two amphipod families Anisogammaridae and Gammaridae. The Gammaridae is characterized by gnathopods of dissimilar size (males), palms oblique and with simple spines and slender simple dactyls. They also have simple coxal gills without accessory lobes and urosome segments with posterodorsal spines in groups of three (Bousfield 1979). The Anisogammaridae, on the other hand, have gnathopods that are morphologically subsimilar, have palms with margins vertical and lined with blunt spines and massive dactyls with posterior accessory blades. They also have coxal gills with accessory lobes and urosome segments with posterodorsal spines in clusters of two or four (Bousfield 1979, 2001). The Gammaridae includes three species in the genus *Gammarus* locally, none of which are certain to be native (Chapman 2007). The Anisogammaridae includes seven local species including one in the genus *Anisogammarus*, four in the genus *Ramellogammarus* and two in *Eogammarus* (Chapman 2007).

The genus *Eogammarus* is characterized by uropods one and two with rami linear and with apical margins spinose, urosome segments one and two with 2–4 groups of spines and peduncular segments one and two with 2–3 groups of posterior marginal setae (Bousfield 1979). The only other species of *Eogammarus* in the northeastern Pacific region is *Eogammarus oclairi*, a pelagic estuarine form very like *E. confervicolus*. Both have robust setae on article one of antenna two and no marginal setae on the palp of article one on maxilla

one. They can be differentiated by each telson lobe, which has two terminal setae, in *E. oclairi*, not one as in *E. confervicolus* (Bousfield 1979). Additional characters include the following (see Tomikawa et al. 2006): aesthetasc of flagellum on antenna one is equal to setae in *E. confervicolus* and longer in *E. oclairi*; female calceoli on antenna two are absent in the former species and present in the latter; the longest setae on pereopod six is half the width of the ischium in the former and shorter in the latter species; and the robust telson setae are equal to or shorter than the slender setae in *E. confervicolus*, but longer in *E. oclairi* (Tomikawa et al. 2006). Despite these characters, it remains a possibility that *E. confervicolus* and *E. oclairi* are the same species and the above variations are simply due to individual size (Chapman 2007).

Members of the closely related genus *Anisogammarus* have first antenna shorter than the second (the most distinctive character) (Bousfield 1979). In *Anisogammarus*, each of the urosomites has a prominent median tooth and a smaller pair of dorsolateral teeth, not 2–4 groups of spines as in *Eogammarus*. Finally, on uropod three, the rami are subequal, not disparate in size as in *Eogammarus*. *Anisogammarus pugettensis* has a prominent fixed median spine on its second urosomite and no rows of spines (Bousfield 2001).

Another closely related genus is *Ramellogammarus*, characterized by dorsal groups of spines on its pleon segments: groups of 1–3 on urosomes one and two; urosome three with 1–2 posterodorsal groups of spines; and 1–4 groups of posterior marginal setae on peduncle segments of both first and second antennae (Bousfield 1979; Bousfield and Morino 1992; Chapman 2007). *Ramellogammarus oregonensis* and *R. ramellus* were both previously members of *Gammarus*, *Anisogammarus* and *Eogammarus*. *Ramellogammarus oregonensis* is strongly armed on pleonites 1–3, while *R. ramellus* has a single posterior seta on pleon plate three (Bousfield and Morino 1992). The two other species in the genus *Ramellogammarus* are freshwater species, *R. columbianus*, and *R. littoralis* (Chapman 2007).

Ecological Information

Range: Type locality is in California (Tomikawa et al. 2006), but specific locale was not found. Known range includes San Diego, California to Alaska.

Local Distribution: Local distribution includes sites in South Slough (e.g. *Salicornia* marsh and Metcalf Preserve). Also occurs on log booms and in mud (e.g. South Slough, Siltcoos River, Siuslaw Estuary) (Barnard 1954).

Habitat: Muddy substrates. *Eogammarus confervicolus* gets name from the "conferva" or long green algae on which it lives. Also occurs with *Salicornia*, *Carex* and *Fucus* (Straude 1987). Growth of *E. confervicolus* was compared between three habitats and ranked as follows: highest in an embankment along the perimeter of a marsh, medium along the edge of a *Fucus* community and lowest in habitat dominated by woody debris (Stanhope and Levings 1985). Little migration occurs between different adjacent substrates, and can result in genetically different races (Stanhope et al. 1992; Stanhope et al. 1993).

Salinity: Full salt water to brackish water (range 5–25, Stanhope et al. 1993).

Temperature:

Tidal Level: Intertidal to 30 meter depths (Bousfield 1979; Chapman 2007). Occurs in drainage channels in South Slough of Coos Bay (+1.4 meters).

Associates: Associates include the isopod, *Gnorimosphaeroma insulare*, (South Slough of Coos Bay) and the amphipod, *Corophium slamonis* (Siuslaw Estuary).

Abundance: Often occurs in great numbers and is the most common gammaroidean amphipod on the Pacific coast of North America (Bousfield 1979). Up to 25,000 individuals per m² comprising 5% of total benthic fauna in June and 17% in August (Sixes River, Martin 1980). Populations can increase rapidly, as was found in Suisun Marsh, California, where *E. confervicolus* were introduced to a wetland pond in September and became a numerically dominant member of the pond by February (Batzer and Resh 1992).

Life-History Information

Reproduction: Most amphipods have separate sexes with some sex determination correlated with environmental conditions

(Straude 1987). Females brood embryos in an external thoracic brood chamber and irrigate embryos with a flow of water produced by pleopod movement. Development within this brood chamber is direct and individuals hatch as juveniles that resemble small adults, with no larval stage. The reproduction and development of *E. confervicolus* was described by Rappaport (1960).

Reproductive behavior and coupling occurs nine days prior to mating. Females are ovigerous from October to December and, again, from June to August (Bousfield 1979). Brood size ranges from 10 to 75 embryos and duration within the brood is 17 days at 10°C and a salinity of 15 (Straude 1987).

Larva: Since most amphipods are direct developing, they lack a definite larval stage. Instead this young developmental stage resembles small adults (e.g. Fig. 39.1, Wolff 2014).

Juvenile:

Longevity:

Growth Rate: Amphipod growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens (Ruppert et al. 2004).

Food: Detritus, particularly from algal or vascular plant material. Research has shown that *E. confervicolus* will readily ingest *Zostera marina* leaves (Harrison 1982), *Enteromorpha linza* and *Pylaiella littoralis* (Pomeroy and Levings 1980) and individuals are capable of ingesting up to 0.21 mg *Ulva* per individual per day (Price and Hylleberg 1982). Ingestion of different algal substrates (e.g. *Fucus distichus* and *Pelvetia fastigiata*) can manifest distinct pheromones between substrate-specific, but geographically close, populations (Stanhope et al. 1992).

Predators: Fish (e.g. juvenile salmonids, Parsons 1985), birds and mallards (Batzer et al. 1993).

Behavior:

Bibliography

1. BARNARD, J. L. 1954. Marine amphipoda of Oregon. Oregon State Monographs, Studies in Zoology. No. 8:1-103.
2. BATZER, D. P., M. MCGEE, V. H. RESH, and R. R. SMITH. 1993. Characteristics of invertebrates

- consumed by mallards and prey response to wetland flooding schedules. *Wetlands*. 13:41-49.
3. BATZER, D. P., and V. H. RESH. 1992. Macroinvertebrates of California seasonal wetland and responses to experimental habitat manipulation. *Wetlands*. 12:1-7.
 4. BOUSFIELD, E. L. 1979. The amphipod superfamily Gammaroidea in the northeastern Pacific region: systematics and distributional ecology. *Bulletin of the Biological Society of Washington*. 3:297-357.
 5. —. 2001. The amphipod genus *Anisogammarus* (Gammaroidea: Anisogammaridae) on the Pacific coast of North America. *Amphipacifica*. 3:29-47.
 6. BOUSFIELD, E. L., and H. MORINO. 1992. The amphipod genus *Ramellogammarus* in fresh waters of western North America: systematics and distributional ecology. Royal British Columbia Museum.
 7. CHAPMAN, J. W. 2007. Amphipoda: Gammaridea, p. 545-611. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 8. HARRISON, P. G. 1982. Control of microbial growth and of amphipod grazing by water soluble compounds from leaves of *Zostera marina*. *Marine Biology*. 67:225-230.
 9. MARTIN, J. T. 1980. Oregon Department of Fish and Wildlife studies of Oregon coastal chinook salmon. *In: Federal Aid Progress Reports: Fisheries Research and Development Section*.
 10. PARSONS, T. R., J. C. SHARP, and W. K. W. LI. 1985. The cultivation of marine amphipods and their use as food for young salmonids. *Zeitschrift fuer Angewandte Ichthyologie*. 1:77-84.
 11. POMEROY, W. M., and C. D. LEVINGS. 1980. Association and feeding relationships between *Eogammarus confervicolus* (Amphipoda: Gammaridae) and benthic algae on Sturgeon and Robert's Banks, Fraser River Estuary. *Canadian Journal of Fisheries and Aquatic Sciences*. 37:1-10.
 12. PRICE, L. H., and J. HYLLEBERG. 1982. Algal-faunal interaction in a mat of *Ulva fenestrata* in False Bay, Washington. *Ophelia*. 21:75-88.
 13. RAPPAPORT, R. 1960. The origin and formation of blastoderm cells of gammarid crustacea. *Journal of Experimental Zoology*. 144:43-59.
 14. RUPPERT, E.E., R.S. FOX, and R.D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*, 7th Edition. Thomson Brooks/Cole, Belmont, CA.
 15. STANHOPE, M. J., M. M. CONNELLY, and B. HARTWICK. 1992. Evolution of a crustacean chemical communication channel: behavioral and ecological genetic evidence for a habitat modified, race specific pheromone. *Journal of Chemical Ecology*. 18:1871-1887.
 16. STANHOPE, M. J., B. HARTWICK, and D. BAILLIE. 1993. Molecular phylogeographic evidence for multiple shifts in habitat preference in the diversification of an amphipod species. *Molecular Ecology*. 2:99-112.
 17. STANHOPE, M. J., and C. D. LEVINGS. 1985. Growth and production of *Eogammarus confervicolus* (Amphipoda: Anisogammaridae) at a log storage site and in areas on undisturbed habitat within the Squamish Estuary, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*. 42:1733-1740.
 18. STRAUDE, C. P. 1987. Phylum or Subphylum Crustacea, Class Malacostraca, Order Amphipoda, p. 424-431. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 19. TOMIKAWA, K., H. MORINO, J. TOFT, and S. F. MAWATARI. 2006. A revision of *Eogammarus birstein*, 1933 (Crustacea, Amphipoda, Anisogammaridae), with a description of a new species. *Journal of Natural History*. 40:1083-1148.

20. WOLFF, C. 2014. Amphipoda, p. 206-209. *In*: Atlas of crustacean larvae. J.W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.

Updated 2015

Grandidierella japonica

A brackish water amphipod

Phylum: Arthropoda, Crustacea
Subphylum: Malacostraca
Order: Amphipoda, Gammaridea
Family: Aoridae

Description

Size: Males up to 22 mm in length, females 13 mm long (San Francisco Bay, Chapman and Dorman 1975; Myers 1981). The illustrated specimen (a male, from Coos Bay) is 10 mm in length (Fig. 1).

Color: Black head, mottled grey to grey brown body (Chapman and Dorman 1975) with distal parts of limbs white (Stephensen 1938; Chapman 2007). This specimen white (preserved in ETOH).

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) or cephalothorax includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six pairs of pleopods. The first three sets of pleopods are generally used for swimming, while the last three are simpler and surround the telson at the animal posterior. The gammarid family Aoridae is characterized by separate urosome articles and a biramous third uropod. They also have a short (sometimes absent) rostrum, a long first antenna and a fleshy telson. *Grandidierella japonica* (see plate 262A, Chapman 2007), however, resembles the family Corophiidae more closely due to the uniramous uropod three (Chapman 2007).

Cephalon:

Rostrum:

Eyes: A single, oval-shaped, lateral eye (Kozloff 1974) that are black and medium in size (Stephensen 1938) (Fig. 1).

Antenna 1: The first antenna in males is more than ½ body length (Chapman and Dorman 1975) and is much shorter in females. The peduncle is with short accessory flagellum in both sexes (Fig. 1b). The male flagellum has 20 articles and is a little longer than peduncle. The female flagellum is equal to peduncle and consists of 18 articles (Stephensen 1938). Male antenna

one longer than its antenna two (Barnard 1973), however female antennae are of equal size (Stephensen 1938) (female not figured).

Antenna 2: Length from ¾ of to longer than antenna one (Chapman and Dorman 1975) (see **antenna 1**). Spines present on peduncle articles 3–5. Male second antenna stout and flagellum with seven articles (Stephensen 1938). Female second antenna length in equal to antenna one and fifth article of peduncle with four strong spines. Female flagellum with six articles (not figured).

Mouthparts: Mandible with large molar, toothed lacinia mobilis, incisors and long 2-articled mandibular palp with third article setose. Maxilliped with 4-articled palp, article four claw-like and article two twice the length of one and two (Chapman and Dorman 1975). Outer maxilliped plates twice the length of inner plates.

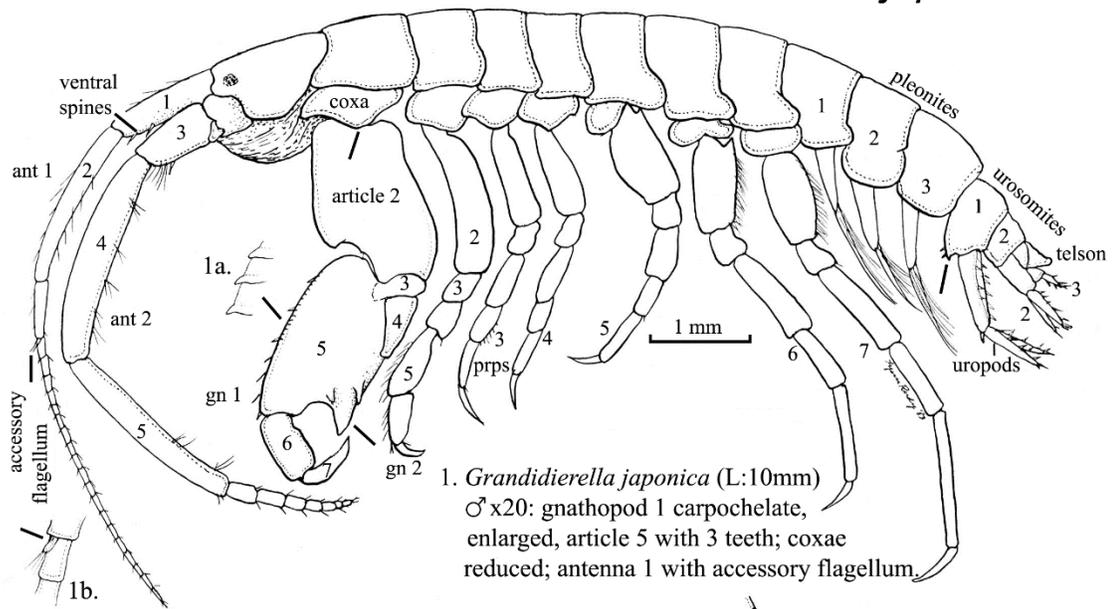
Pereon:

Coxae: Reduced (Chapman and Dorman 1975), serially arranged and barely contiguous (Barnard 1973) (Fig. 1). Coxal plate one with a medial-ventral tooth (Chapman and Dorman 1975) (just slightly produced in illustrated specimen).

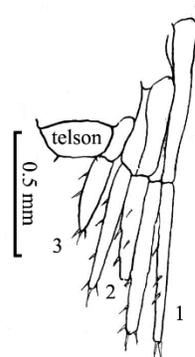
Gnathopod 1: Male gnathopod one is greatly enlarged, “carpochelate” (i.e. not filtering type) (*Grandidierella*, Barnard 1973; Chapman 2007). Articles two and five greatly enlarged and subequal (Chapman and Dorman 1975). Article two oval, article three small, article four small and elongate. Article five with sides parallel and with one enlarged tooth forming thumb and two smaller teeth (*Grandidierella*, Barnard 1975). Anterior edge of article five with 18–20 transverse fine ridges (“stridulating organs”, Stephensen 1938) and four spines (Figs. 1, 1a). Female gnathopod one is small, but larger than gnathopod two. Article two is setose and narrow (Stephensen 1938) (Fig. 5).

Gnathopod 2: Male gnathopod two is simple and much smaller than gnathopod

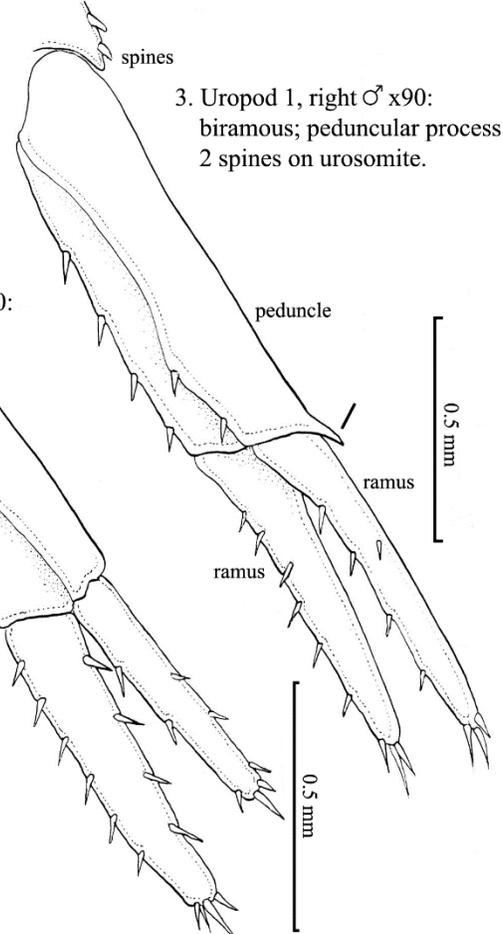
Grandidierella japonica



1. *Grandidierella japonica* (L:10mm)
 ♂ x20: gnathopod 1 carpocheate,
 enlarged, article 5 with 3 teeth; coxae
 reduced; antenna 1 with accessory flagellum.

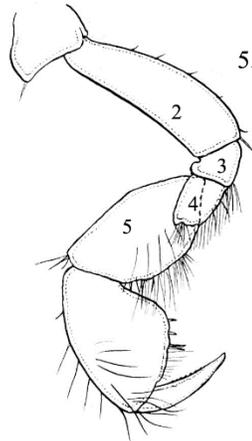


2. Telson and right uropods ♂ x50: telson button-like.

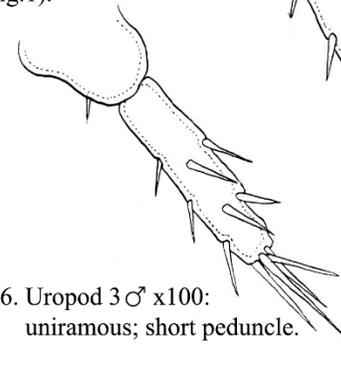


3. Uropod 1, right ♂ x90: biramous; peduncular process; 2 spines on urosomite.

4. Uropod 2 ♂ x100: biramous, thin.



5. Gnathopod 1 ♀: article 2 narrow (from Stephens 1938, Fig. 1).



6. Uropod 3 ♂ x100: uniramous; short peduncle.

one. Article two is twice the length of article five. Article three is short and dactyl is not chelate (Fig. 1). Female gnathopod two is setose, is smaller than gnathopod one and with article two about 2/3 length of male article two (Barnard 1973).

Pereopods 3 through 7: Simple, not prehensile (Barnard 1973) and increasing in length. A character of the Aoridae is a seventh pereopod that is longer than the sixth (see plate 269C, Chapman 2007) and the seventh pereopod in *G. japonica* is very long (Fig. 1). Female pereopods are with narrow second articles (Stephensen 1938).

Pleon:

Pleonites: Third pleonite is without dorsal tooth (Barnard 1975)

Urosomites: All three urosomites short (Fig. 1). The first uropod is biramous and longer than the second or third. The peduncle is with peduncular process and two anterolateral spines on urosomite (Barnard 1969) (Fig. 3). Second uropod is also biramous (*Grandidierella*, Barnard 1975) and with thin peduncle and long rami (Barnard 1975) (Fig. 4). The third uropod is uniramous, without hooked apical spine or long setae (Barnard 1975) (a defining character of *G. japonica*). It is not fleshy, blunt or elongate and the ramus is three times as long as the peduncle (Barnard 1973) (Fig. 6).

Epimera:

Telson: Telson uncleft and somewhat swollen (Kozloff 1974), with button-like morphology and medial groove (Chapman and Dorman 1975) (Figs. 1, 2).

Sexual Dimorphism: Male first gnathopod article two is expanded and article five is large, with parallel sides, teeth and stridulating organ. All features are lacking in females. Male antenna one is also longer than two and female antennae are equal.

Possible Misidentifications

The Aoridae are a family of gammarid amphipods that are tube-building suspension feeders found in marine and estuarine habitats. They are characterized by a short rostrum, long first antenna, gnathopod one larger than two (in males), a fleshy telson, a long seventh pereopod (longer than the sixth), distinctly separate urosome articles and a biramous uropod three. There are four aorid amphipod species that are not native to the

northeastern Pacific coast (e.g. *Aoroides secundus*, *Microdeutopus gryllotapla*), one of which is *G. japonica*. At least two aorid genera that are quite similar to *Grandidierella*: *Paraoroides*, and *Aoroides* (family Aoridae). *Paraoroides* species have a uniramous third uropod (as in *G. japonica*), but this ramus is only as long as the peduncle, not twice or three times as long (Barnard 1973). In *Paraoroides*, the first gnathopod is not carpochele, but only slightly enlarged, the gnathopods are equal in size. The third article of the first antenna is not elongate, as it is in *G. japonica*. *Aoroides* species (six local) have an immensely merocelate male first gnathopod (Barnard 1975), quite different from that of *G. japonica*. Article four is elongate, article five is oval, but lacks teeth. The gnathopod is the filtering type, with long setae. The third uropods in this genus are biramous, not uniramous as in *Grandidierella*. *Aoroides columbiae* is a Pacific coast species. Other species of *Grandidierella* have not been recorded from our area, include a tropical species, *G. nottoni*, and four freshwater species. *Grandidierella japonica* closely resembles amphipods in the family Corophiidae (Chapman 2007)

The gammarid family Corophiidae is characterized by individuals that build U-shaped tubes in both soft sediments and on hard surfaces, sometimes forming dense aggregations. Species can be dramatically sexually dimorphic and, while males may be easier to identify with taxonomically relevant characters including the rostrum and peduncle of second antennae, most females can be reliably identified to species as well (Chapman 2007). Five corophiid genera occur locally, *Americorophium*, *Corophium*, *Crassicorophium*, *Laticorophium* and *Monocorophium*. The three common estuarine species in this guide (*A. brevis*, *A. salmonis*, *A. spinicorne*) were previously members of the genus *Corophium* (see Shoemaker 1949), but were transferred to the genus *Americorophium* in 1997 (Bousfield and Hoover 1997).

Other common gammarid families include the Ampithoidae, Cheluridae, Ischyroceridae, Podoceridae, and Isaeidae (for key see Chapman 2007). The Ampithoidae have a poorly recessed head (Barnard 1973) and a short third article on the

peduncle of antenna one. At least one ramus of the third uropod in this family is very setose terminally and the third uropod also has curved hooks on the end of its stout ramus (Barnard 1975). The Ampithoidae have a thick, uncleft telson. In our area there are several species of *Ampithoe* including *A. lacertosa* and *A. valida*. The Cheluridae are a wood-boring group that utilize the holes in wood left by boring isopods family with a huge dorsal tooth on the third pleonite. The urosomites form a box-like structure, and the second uropods are “flabellate” (i.e. paddle-like). *Chelura terebrans* is an introduced species found on the Pacific coast and is the only chelurid species found in this region (Chapman 2007). The Ischyroceridae is another closely related family. Members have an unusual thorn-like rostrum and a rather cylindrical body. The telson is broad and short, and it is the second male gnathopod, not the first, in this family which is carpochele. Ischyroceridae have hooks on the outer ramus of the third uropod (like Ampithoidae), but this ramus is short and slender, not stout. The inner ramus is also slender and void of setae. Local genera include *Cerapus*, *Erichthonius*, *Jassa*, *Ischyrocerus*, *Microjassa* and *Ruffojassa*. *Erichthonius* species have a body much like *G. japonica*, but the first male gnathopod is normal, and the second is carpochele (the opposite is true for *Grandidierella*). At least two species occur in our area, *E. rubicornis* (= *E. hunteri*) and *E. brasiliensis*. In Podoceridae both gnathopods (especially the second) are large and subchelate. The first urosomite is very long, more than twice the length of the second. The genera *Podocerus*, *Dulichia*, and *Dyopedos* occur in our area. The Isaeidae are marine, tube building suspension feeders and include the common genus *Photis*. Characteristics of this group include a recessed head, and an elongate third article on the first antenna (like *G. japonica*). *Photis* species have elongate coxae and a normal first gnathopod, but an enlarged second gnathopod that is often highly sculptured. The third uropod has an elongate peduncle.

Ecological Information

Range: *Grandidierella japonica* is native to Abasiri River, Hokkaido, Japan, from which it

was introduced to U.S. Pacific harbors with *Crassostrea* (commercial oyster), Tomales, Bolinas, and San Francisco, California, possibly as early as 1928 (Chapman and Dorman 1975). Current distribution includes the Fraser River, Canada, Bahia San Quintin, Hawaii, England and Australia in addition to the northeast Pacific (Chapman 2007). For west coast invasion history, see Fig. 1, Pilgrim et al. 2013. Genetic barcoding data suggests two cryptic *G. japonica* species – both present in San Francisco Bay with one expanding northward and the other southward (Pilgrim et al. 2013).

Local Distribution: Coos Bay sites include the South Slough and North Bend Airport (Gonor 1979).

Habitat: Burrows in mud bottoms of bays and estuaries where individuals build U-shaped tubes, in which pairs can often be found (Chapman and Dorman 1975). Males also found out of tubes and in tide pools at low tide. *Grandidierella japonica* is sensitive to a variety of pollutants and is a common subject of toxicity tests (e.g. Nipper et al. 1989).

Salinity: Brackish water in Japan and introduced into Oregon and California estuaries (Chapman and Dorman 1975). Unique osmoregulatory tissue of the coxal gills allow *G. japonica* to exist in a wide variety of salinities (Kikuchi and Matsumasa 1993).

Temperature:

Tidal Level: Intertidal to 10 meters (Chapman 2007). Collected at +1.5 meters MLLW in South Slough.

Associates: Introduced with *Crassostrea*. In South Slough, associates include the algae, *Enteromorpha* sp., the amphipod, *Ampithoe valida*, and sacoglossan, *Aplysiopsis smithi*. California associates include polychaetes, *Harmothoe* sp., *Heteromastus* sp., *Capitella* sp., *Neanthes* sp., *Streblospio* sp., molluscs, *Mya* sp., *Cryptomya* sp., *Macoma* sp., barnacles, *B. improvisus*, isopods, *Gnorimosphaeroma lutea*, amphipods, *Photis* sp., *Corophium* sp., *Allorchestes* sp., *Ampithoe* sp., *Anisogammarus* sp. and the anemone *Haliplanella* sp. (Chapman and Dorman 1975).

Abundance: Can be present in great numbers seasonally. Third most common amphipod at North Bend Airport site (Gonor

1979). South Slough, abundances of 27 individuals per m² reported (Posey 1985).

Life-History Information

Reproduction: Most amphipods have separate sexes with some sex determination correlated with environmental conditions (Straude 1987). Females brood embryos in an external thoracic brood chamber and irrigate embryos with water produced by pleopod movement. Development within this brood chamber is direct and individuals hatch as juveniles that resemble small adults, with no larval stage. Little is known about the reproduction and development in *G. japonica* (but see Wang et al. 2009, in Chinese).

Larva: Since most amphipods are direct developing, they lack a definite larval stage. Instead this young developmental stage resembles small adults (e.g. Fig. 39.1, Wolff 2014).

Juvenile:

Longevity:

Growth Rate: Amphipod growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: Detritivore that feeds on epiphytes and suspended particles. Also known to be a predator of amphipods and can be cannibalistic (Chapman 2007).

Predators: The benthic carnivorous fish *Clevelandia ios*, *Hypsopsetta guttulata*, *Gillichthys mirabilis*, *Fundulus parvipinnis* (Tijuana estuary, West et al. 2003).

Behavior: Builds U-shaped tubes which protrude from the mud (Chapman and Dorman 1975) and modify native habitats (Pilgrim et al. 2013).

Bibliography

1. BARNARD, J. L. 1969. Gammaridean amphipoda of the rocky intertidal of California: Monterey Bay to La Jolla. Smithsonian Institution Press, Washington.
2. —. 1973. Revision of Corophiidae and related families (Amphipoda). Smithsonian Institution Press, Washington, D.C.
3. —. 1975. Phylum Anthropoda: Crustacea, Amphipoda: Gammaridea, p. 313-366. *In*: Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
4. BOUSFIELD, E. L., and P. M. HOOVER. 1997. The amphipod superfamily Corophioidea on the Pacific coast of North America. Part 5. Family Corophiidae: Corophiinae, new subfamily. Systematics and distributional ecology. *Amphipacifica*. 2:67-139.
5. CHAPMAN, J. W., E. L. BOUSFIELD, and D. E. BOWERS. 2007. Amphipoda: Gammaridea, p. 545-618. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
6. CHAPMAN, J. W., and J. A. DORMAN. 1975. Diagnosis systematics and notes on *Grandidierella japonica* new-record Amphipoda: Gammaridea and its introduction to the Pacific coast of the USA. *Bulletin Southern California Academy of Sciences*. 74:104-108.
7. GONOR, J. J., D. R. STREHLOW, and G. E. JOHNSON. 1979. Ecological assessments at the North Bend airport extension site. School of Oceanography, Oregon State University, Salem, OR.
8. KIKUCHI, S., and M. MATSUMASA. 1993. The osmoregulatory tissue around the afferent blood vessels of the coxal gills in the estuarine amphipods, *Grandidierella japonica* and *Melita setiflagella*. *Tissue and Cell*. 25:627-638.
9. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
10. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In*: The Light and Smith manual: intertidal

- invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
11. MYERS, A. A. 1981. Taxonomic studies on the genus *Grandidierella* new-record Crustacea: Amphipoda 3. Fijian, Australian and Saudi-Arabian species. Bulletin du Museum National d'Histoire Naturelle Section A Zoologie Biologie et Ecologie Animales. 3:213-226.
 12. NIPPER, M. G., D. J. GREENSTEIN, and S. M. BAY. 1989. Short-term and long-term sediment toxicity test methods with the amphipod *Grandidierella japonica*. Environmental Toxicology and Chemistry. 8:1191-1200.
 13. PILGRIM, E. M., M. J. BLUM, D. A. REUSSER, H. I. LEE, and J. A. DARLING. 2013. Geographic range and structure of cryptic genetic diversity among Pacific North American populations of the non-native amphipod *Grandidierella japonica*. Biological Invasions. 15:2415-2428.
 14. POSEY, M. H. 1985. The effects upon the macrofaunal community of a dominant burrowing deposit feeder, *Callinassa californiensis*, and the role of predation in determining its intertidal distribution. Ph.D. University of Oregon.
 15. SHOEMAKER, C. R. 1949. The amphipod genus *Corophium* on the west coast of America. Journal of the Washington Academy of Sciences. 89:66-82.
 16. STEPHENSEN, K. 1938. *Grandidierella japonica* n. sp. A new amphipod with stridulating (?) organs from brackish water in Japan. Annotationes zoologicae Japonenses. 17:179-184.
 17. STRAUD, C. P. 1987. Phylum or Subphylum Crustacea, Class Malacostraca, Order Amphipoda, p. 424-431. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathman (ed.). University of Washington Press, Seattle, WA.
 18. WANG, R., D. GUAN, Q. YAN, M. HAN, H. CHEN, and J. YAN. 2009. Life history of amphipod *Grandidierella japonica* cultured in laboratory. Marine Environmental Science. 28:272-274.
 19. WEST, J. M., G. D. WILLIAMS, S. P. MADON, and J. B. ZEDLER. 2003. Integrating spatial and temporal variability into the analysis of fish food web linkages in Tijuana Estuary. Environmental Biology of Fishes. 67:297-309.
 20. WOLFF, C. 2014. Amphipoda, p. 206-209. *In*: Atlas of crustacean larvae. M. J.W., J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.

Updated 2015

Americorophium brevis

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Amphipoda, Gammaridea
Family: Corophiidae

Taxonomy: *Corophium brevis* was described in 1949 by Shoemaker and was transferred to the genus *Americorophium* in 1997 based on morphological characters (Bousfield and Hoover 1997) (see **Possible Misidentifications**). Not all researchers have followed this transition in other *Americorophium* species (e.g. *A. spinicorne*, Lester and Clark 2002; Sakamaki and Richardson 2009), but we follow the nomenclature used in other current local intertidal guides (Chapman 2007).

Description

Size: Males range in size from 3.5 (Shoemaker 1949) to 8 mm (South Slough of Coos Bay). Females are 4 (Siuslaw Estuary) to 4.5 mm (Shoemaker 1949).

Color: Transparent, with brown mottled markings, especially on large second antenna.

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six segments comprising three **pleonites** (together the pleosome), three **urosomites** (together the urosome), and finally a **telson** at the animal posterior (see Plate 254, Chapman 2007). In members of the genus *Americorophium*, the body is flattened dorso-ventrally and rarely exceeds 1 cm in total length (including antennae) in local specimens (see Fig 46, Kozloff 1993).

Cephalon:

Rostrum: Small central triangle is shorter than sharp ocular spines (Fig. 1).

Eyes:

Antenna 1: Reaches a little beyond fourth article of second antenna in males and the flagellum ranges from approximately 11 joints (Siuslaw Estuary specimens) to 9–14 (Coos Bay specimens, Fig. 1) (Shoemaker 1949). Antenna base is not expanded

laterally. The female flagellum consists of 7–8 joints and is almost as long as second antenna (Shoemaker 1949) (Fig. 6).

Antenna 2: Male antenna large, almost as long as body and is with groups of setae. The fourth article is a large, distal tooth forming a half-moon with an accessory tooth within (Fig. 2). The fifth article has two small teeth: one distal and one proximal (Fig. 2). The second antenna in females is not as large as in males, and instead of a half-moon tooth and an accessory tooth, there are three pairs of equally spaced, heavy spines on the lower margin (Shoemaker 1949) (Fig. 5).

Mouthparts:

Pereon:

Coxae:

Gnathopod 1:

Gnathopod 2: Filtering type, with fine long setae, present in both sexes (Fig. 3).

Pereopods 3 through 7: Quite setose.

Pleon:

Pleonites:

Urosomites: Three segments of urosome separate and distinguishable (Fig. 4) in both sexes. The lateral edge of peduncle with about eight short, blunt spines on first uropods (Fig. 4). Third uropods with few fine setae, on distal end only, in both sexes (Fig. 4).

Epimera:

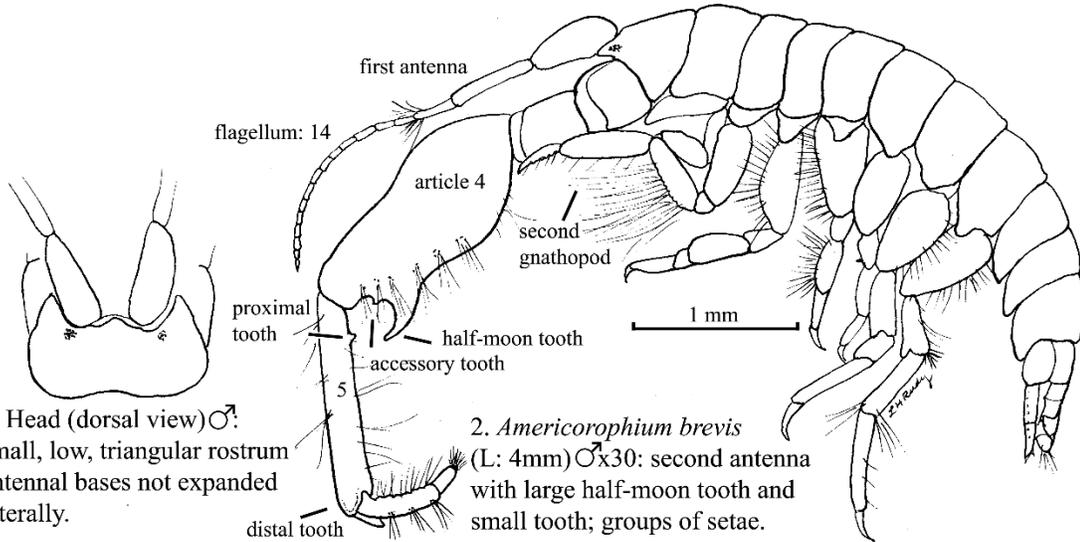
Telson: Posterior rounded and convex with parallel rows of spines (Fig. 4).

Sexual Dimorphism: Males and females exhibit differing morphology in characters of Antenna 1 and 2 as well as overall body size.

Possible Misidentifications

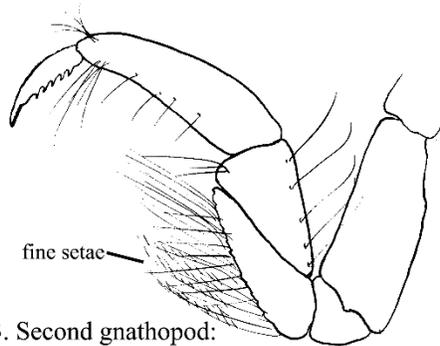
The gammarid family Corophiidae is characterized by individuals that build U-shaped tubes in both soft sediments and on hard surfaces, sometimes forming dense aggregations. Species can be dramatically sexually dimorphic and, although males may be easier to identify with taxonomically relevant characters including the rostrum and peduncle of second antennae, most females can be reliably identified to species as well

Americorophium brevis

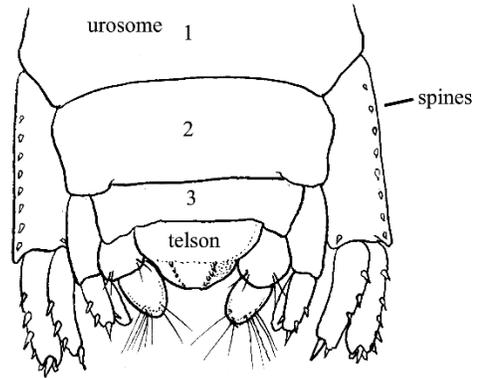


1. Head (dorsal view) ♂:
small, low, triangular rostrum
antennal bases not expanded
laterally.

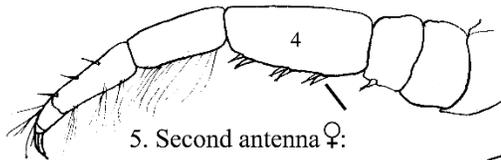
2. *Americorophium brevis*
(L: 4mm) ♂x30: second antenna
with large half-moon tooth and
small tooth; groups of setae.



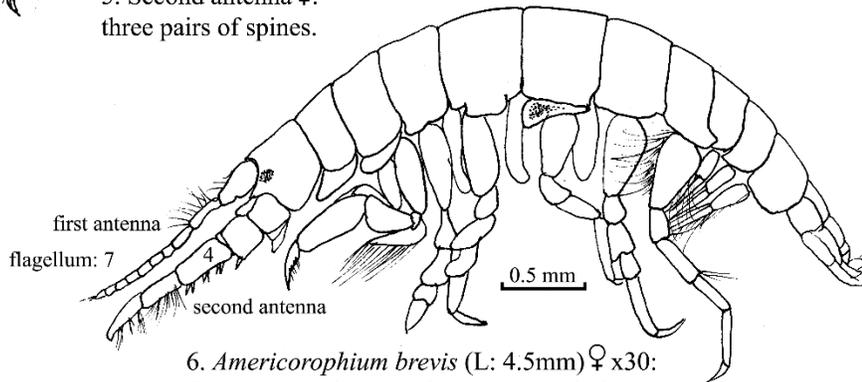
3. Second gnathopod:
"filtering" type.



4. Urosome and telson ♂:
three distinct segments, telson convex,
with rows of small spines; first uropods
with eight small spines.



5. Second antenna ♀:
three pairs of spines.



6. *Americorophium brevis* (L: 4.5mm) ♀ x30:
first antenna almost as long as second; three
pairs of spines on article four, below.

(Chapman 2007). Five corophiid genera occur locally, *Americorophium*, *Corophium*, *Crassicorophium*, *Laticorophium* and *Monocorophium*. The three common estuarine species in this guide (*A. brevis*, *A. salmonis*, *A. spinicorne*) were previously members of the genus *Corophium* (see Shoemaker 1949), but were transferred to the genus *Americorophium* in 1997 (Bousfield and Hoover 1997).

All *Americorophium* species have filtering-type second gnathopods and long setae on the third uropods. Of the four local *Americorophium* species, sexual dimorphism is strong in the three species *A. brevis*, *A. salmonis*, and *A. stimpsoni*. In particular, the second antenna and fourth segment differ between males and females (Shoemaker 1949). This is not the case, however, for the fourth *Americorophium* species, *A. spinicorne*, where male and female morphologies are similar. Additional characteristics that differ between species (particularly *A. brevis* and *A. salmonis*) include first antenna, telson, first uropods and third uropods.

Americorophium stimpsoni, principally a northern California species, does not seem to occur in Oregon. Its chief key characteristic is a prominent male rostrum, almost as long as the ocular lobes. The females are much like those of *A. salmonis*.

Americorophium spinicorne, another prominent northwest species, has less sexual dimorphism than other *Americorophium* species. Both males and females have a half-moon tooth on the fourth article of the second antenna, but without the small accessory tooth. *Americorophium spinicorne* is also strongly euryhaline and often found in fresh-water habitats. Segments of urosome are separate and not fused in *A. spinicorne* and males and females can be distinguished by the second antennal features and by the presence of lamellae and/or eggs in females.

Males: Of the *Americorophium* species in which males have urosome segments dissimilar to females, *A. stimpsoni*, *A. brevis*, and *A. salmonis* all have a half-moon and accessory tooth on the fourth article of the second antenna. *Americorophium brevis* and *A. salmonis* often have similar rostrums, but that of *A. stimpsoni* has a prominent central lobe nearly as long as the ocular lobes. In *A. salmonis* the first

antenna reaches only to the middle of the fourth article. *Americorophium brevis* does not have the flat expanded first articles of the first antenna and *A. salmonis* usually has 14–16 articles in the flagellum, (though occasional specimens will have 11–12). In *A. brevis*, the males have about 11 articles in the flagellum of the first antenna. The uropods of *A. salmonis* and *A. brevis* are quite dissimilar. In *A. salmonis*, the peduncle of the first uropod is armed on the outside edge with three to six long, slender spines and at the distal edge with two to three short, blunt spines. *Americorophium brevis* has instead only eight short, blunt spines. The third uropods of *A. salmonis* have many more and longer setae than those of *A. brevis*. The telson shape and spination of the two species are also quite different (compare Figs. 4, *A. brevis*, and Fig. 5, *A. salmonis*).

Females: *A. salmonis* and *A. stimpsoni* females are very much alike, with no strong distinguishing characteristics, so the species should not be differentiated solely by female specimens. The only *Americorophium* female of this group to have the half-moon hook is *A. spinicorne*, so this species is easily distinguished from others. *Americorophium brevis* has three pairs of spines, as well as a spine on the gland cone, instead of having two single spines on the underside of the fourth article of the second antenna. The first antenna has eight joints in the flagellum, while that of *A. salmonis* has ten.

Ecological Information

Range: Type locality is Puget Sound, Washington. Known range includes Alaska to San Francisco Bay (Shoemaker 1949; Coyle and Müller 1981).

Local Distribution: Coos Bay estuarine distribution including South Slough. Distribution also known in other Oregon estuaries (e.g. Siuslaw Estuary, Barnard 1954).

Habitat: Members of the Corophiidae inhabit small U-shaped tubes in soft sediments, or on hard surfaces (Chapman 2007). Occurs in muddy habitats (e.g. South Slough) and sometimes in a mud and wood chip mix. Especially abundant in brackish estuaries with a high degree of silt and mud (Raymond et al. 1985; Kozloff 1993). Comparisons of macrofaunal communities within and outside of *Dendraster excentricus* beds found *Americorophium* species to be more prevalent

where sand dollars were not present (Smith 1981). Corophiid amphipods are frequently used in tests of sediment toxicity and/or water quality (e.g. fluoranthene, Swartz et al. 1990).

Salinity:

Temperature:

Tidal Level: A high intertidal species.

Associates: Known associates include tanaidaceans, small polychaetes and other Corophiidae.

Abundance: Populations are often very dense and easily observed or collected in the field. The abundance of *Americorophium* species measured in the Campbell River Estuary ranged from zero to ~15,000–31,000 per square meter in July (Raymond et al. 1985).

Life-History Information

Reproduction: Development in most amphipods is direct, lacking a larval stage, and little is known about the reproduction and development in *A. brevis*. Oviparous *A. brevis* females have been observed in summer months whereas oviparous *A. spinicorne* females have been observed in February, March, May and December (Eriksen 1968). In the European species, *Corophium volutator*, breeding occurs in February (over-wintering population) and again in July–August. Young remain in brood pouch four weeks and females produce up to four broods per year (Green 1968).

Larva: Since most amphipods develop directly, they lack a definite larval stage. Instead the young developmental stage resembles small adults (e.g. Fig. 39.1, Wolff 2014).

Juvenile:

Longevity:

Growth Rate: Amphipod growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens (Ruppert et al. 2004).

Food: A detritovore, *Americorophium brevis* sorts material with filtering gnathopods. Abdominal appendages create a water current that is filtered by the fine hairs on the gnathopods, and the filtrate is then scraped off and ingested (Miller 1984; Kozloff 1993).

Predators:

Behavior: Females often in tubes, while males are out on mud surface

Bibliography

1. BARNARD, J. L. 1954. Marine amphipoda of Oregon. Oregon State Monographs, Studies in Zoology. No. 8:1-103.
2. BOUSFIELD, E. L., and P. M. HOOVER. 1997. The amphipod superfamily Corophioidea on the Pacific coast of North America. Part 5. Family Corophiidae: Corophiinae, new subfamily. Systematics and distributional ecology. Amphipacifica. 2:67-139.
3. CHAPMAN, J. W. 2007. Amphipoda: Gammaridea, p. 545-611. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
4. COYLE, K. O., and G. J. MUELLER. 1981. New records of Alaskan marine crustacea, with descriptions of two new gammaridean amphipoda. Sarsia. 66:7-18.
5. ERIKSEN, C. H. 1968. Aspects of the limno-ecology of *Corophium spinicorne* (Stimpson) (Amphipoda) and *Gnorimosphaeroma oregonensis* (Dana) (Isopoda). Crustaceana. 14:1-12.
6. GREEN, J. 1968. The Biology of estuarine animals. University of Washington Press, Seattle.
7. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
8. LESTER, G. T., and W. H. CLARK. 2002. Occurrence of *Corophium spinicorne* (Stimpson, 1857) (Amphipoda: Corophiidae) in Idaho, USA. Western North American Naturalist. 62:230-233.
9. MILLER, D. C. 1984. Mechanical post-capture particle selection by suspension feeding and deposit feeding *Corophim*. Journal of Experimental Marine Biology and Ecology. 82:59-76.

10. RAYMOND, B. A., M. M. WAYNE, and J. A. MORRISON. 1985. Vegetation, invertebrate distribution, and fish utilization of the Campbell River Estuary, British Columbia, Canada. Canadian Manuscript Report of Fisheries and Aquatic Sciences:1-33.
11. RUPPERT, E.E., R.S. FOX, and R.D BARNES. 2004. Invertebrate Zoology: A Functional Evolutionary Approach, 7th Edition. Thomson Brooks/Cole, Belmont, CA.
12. SAKAMAKI, T., and J. S. RICHARDSON. 2009. Dietary responses of tidal flat macrobenthos to reduction of benthic microalgae: a test for potential use of allochthonous organic matter. Marine Ecology Progress Series. 386:107-113.
13. SHOEMAKER, C. R. 1949. The amphipod genus *Corophium* on the west coast of America. Journal of the Washington Academy of Sciences. 89:66-82.
14. SMITH, A. L. 1981. Comparison of macrofaunal invertebrates in sand dollar (*Dendraster excentricus*) beds and in adjacent areas free of sand dollars. Marine Biology. 65:191-198.
15. SWARTZ, R. C., D. W. SCHULTS, T. H. DEWITT, G. R. DITSWORTH, and J. O. LAMBERSON. 1990. Toxicity of fluoranthene in sediment to marine amphipods: a test of the equilibrium partitioning approach to sediment quality criteria. Environmental Toxicology and Chemistry. 9:1071-1080.
16. WOLFF, C. 2014. Amphipoda, p. 206-209. *In: Atlas of crustacean larvae.* J. H. Martin J.W. Olesen, J.T. (ed.). Johns Hopkins University Press, Baltimore.

Updated 2015

Americorophium salmonis

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Amphipoda, Gammaridea
Family: Corophiidae

Taxonomy: *Corophium salmonis* was among the first corophiid amphipods described in North America (Stimpson 1857). It was transferred to the genus *Americorophium* in 1997 based on morphological characters (Bousfield and Hoover 1997) (see **Possible Misidentifications**). Researchers have not always followed this transition in other *Americorophium* species (e.g. *A. spinicorne*, Lester and Clark 2002; Sakamaki and Richardson 2009), but we follow the nomenclature used in other current local intertidal guides (Chapman 2007).

Description

Size: Largest males are 6 mm in length, from rostrum to end of uropods and the average size range is 4–6 mm (Coos Bay) and 7.5 mm (Siuslaw Estuary). Females are approximately 7 mm in length (Shoemaker 1949). The illustrated specimen (from Coos Bay) is 6 mm.

Color: Males are transparent, with brown mottling, especially on large second antenna (Fig. 3). Females, like other *Americorophium* species, are clear, with brown mottling, especially on the second antennae.

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six segments comprising three **pleonites** (together the pleosome), three **urosomites** (together the urosome), and finally a **telson** at the animal posterior (see Plate 254, Chapman 2007). In members of the genus *Americorophium*, the body is flattened dorso-ventrally and rarely exceeds 1 cm in total length (including antennae) in local specimens (see Fig 46, Kozloff 1993).

Cephalon:

Rostrum: The male rostrum is straight, slightly convex or with low central projection (Fig. 1) (Shoemaker 1949). The female rostrum, on the other hand, is a broad and low triangle (Fig. 7).

Eyes:

Antenna 1: Reaches to middle of article four of second antenna in males. Their flagellum comprises 14–16 articles (occasionally 11–12) and the first article of the peduncle is flat and greatly expanded laterally (Fig. 1) (Shoemaker 1949). First antenna about as long as the second in females. The female flagellum comprises ten joints (Shoemaker 1949) and the first article is not expanded.

Antenna 2: Much longer than body in mature male specimens. The fourth article has large distal tooth, forming a half-moon, and small tooth within (Fig. 3). The fifth article has two teeth below: one at distal end and one near proximal end (Fig. 3). The proximal tooth lies below the flexed half-moon tooth. The gland cone on second article below, is bilobed and elaborate (Fig. 2) (Shoemaker 1949). The second antenna in females is not as massive as in males. The fourth article is without a large half-moon tooth and accessory, but with two single spines on the lower edge and two on the third article (Fig. 4). The gland cone of females is simpler than that of the male and is without lobes (Fig. 8).

Mouthparts:

Pereon:

Coxae: Setose lamellae (pairs of brood plates attached to bases of coxae) are present in females only and are used for holding eggs and young. Do not confuse with fleshy gills, which are also attached to coxae.

Gnathopod 1:

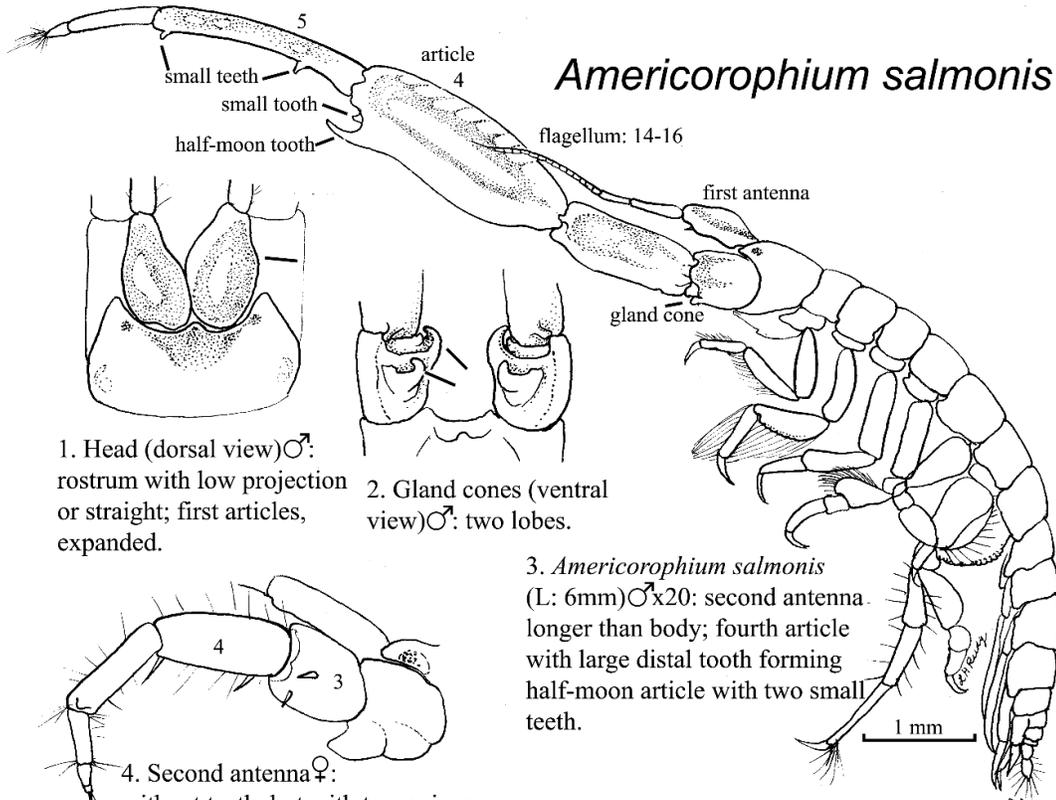
Gnathopod 2: Filtering type, with fine long setae, present in both sexes, morphology as in other *Americorophium* species (see Fig. 3, *A. brevis* in this guide).

Pereopods 3 through 7:

Pleon:

Pleonites:

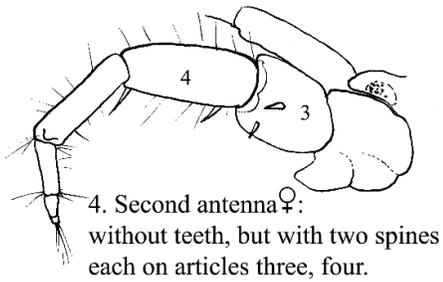
Americorophium salmonis



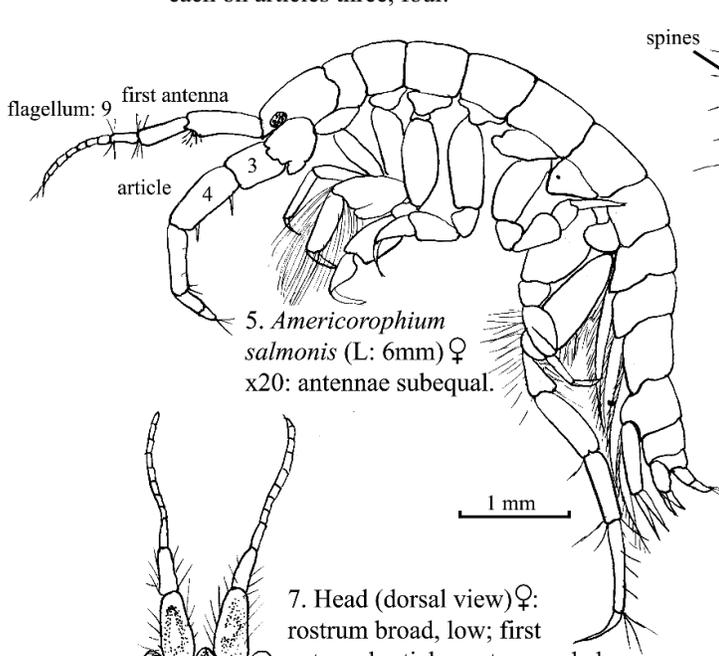
1. Head (dorsal view) ♂: rostrum with low projection or straight; first articles, expanded.

2. Gland cones (ventral view) ♂: two lobes.

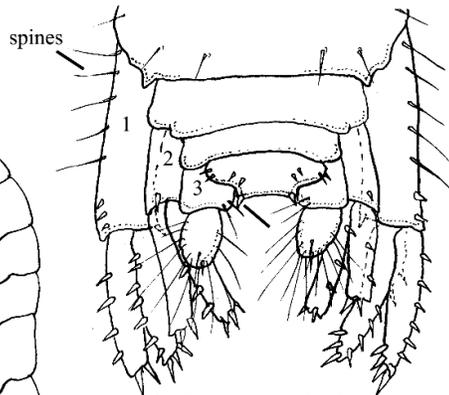
3. *Americorophium salmonis* (L: 6mm) ♂x20: second antenna longer than body; fourth article with large distal tooth forming half-moon article with two small teeth.



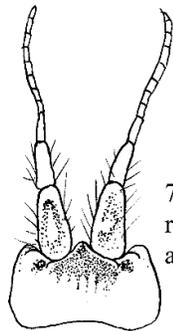
4. Second antenna ♀: without teeth, but with two spines each on articles three, four.



5. *Americorophium salmonis* (L: 6mm) ♀ x20: antennae subequal.



6. Urosome and telson: first uropods with slender, blunt spines; telson margin straight, two spines.



7. Head (dorsal view) ♀: rostrum broad, low; first antennal articles not expanded.



8. Gland cones (ventral view) ♀: simple, lobeless.

Urosomites: Urosome with posterior margin straight, slightly concave and with a spine in each corner as well as two spines on each lateral edge and two on the inside edge (Fig. 6). First uropods with three to six slender spines along outside edge of peduncle. Two to three small, blunt spines present at distal corner (Fig. 6). Third uropods have many slender setae on all edges (Fig. 6).

Epimera:

Telson:

Sexual Dimorphism: Males and females exhibit differing morphology in characters of the rostrum, Antenna 1 and 2, as well as overall body size and color.

Possible Misidentifications

The gammarid family Corophiidae is characterized by individuals that build U-shaped tubes in both soft sediments and on hard surfaces, sometimes forming dense aggregations. Species can be dramatically sexually dimorphic. Although males may be easier to identify with taxonomically relevant characters including the rostrum and peduncle of second antennae, most females can be reliably identified to species as well (Chapman 2007). Five corophiid genera occur locally: *Americorophium*, *Corophium*, *Crassicorophium*, *Laticorophium* and *Monocorophium*. The three common estuarine species in this guide (*A. brevis*, *A. salmonis*, and *A. spinicorne*) were previously members of the genus *Corophium* (see Shoemaker 1949), but were transferred to the genus *Americorophium* in 1997 (Bousfield and Hoover 1997).

All *Americorophium* species have filtering-type second gnathopods and long setae on the third uropods. Of the four local *Americorophium* species, sexual dimorphism is strong in the three species *A. brevis*, *A. salmonis*, and *A. stimpsoni*. In particular, the second antenna and fourth segment differ between males and females (Shoemaker 1949). This is not the case, however, for the fourth *Americorophium* species, *A. spinicorne*, where male and female morphologies are similar. Additional characteristics that differ between species (particularly *A. brevis* and *A. salmonis*)

include first antenna, telson, first uropods and third uropods.

Americorophium stimpsoni, principally a northern California species, does not seem to occur in Oregon. Its chief key characteristic is a prominent male rostrum, almost as long as the ocular lobes. The females are much like those of *A. salmonis*.

Americorophium spinicorne, another prominent northwest species, has less sexual dimorphism than other *Americorophium* species. Both males and females have a half-moon tooth on the fourth article of the second antenna, but without the small accessory tooth. *Americorophium spinicorne* is also strongly euryhaline and often found in fresh-water habitats. Segments of urosome are separate and not fused in *A. spinicorne* and males and females can be distinguished by the second antennal features and by the presence of lamellae and/or eggs in females.

Males: Of the *Americorophium* species in which males have urosome segments dissimilar to females, *A. stimpsoni*, *A. brevis*, and *A. salmonis* all have a half-moon and accessory tooth on the fourth article of the second antenna. *Americorophium brevis* and *A. salmonis* often have similar rostrums, but that of *A. stimpsoni* has a prominent central lobe nearly as long as the ocular lobes. In *A. salmonis* the first antenna reaches only to the middle of the fourth article. *Americorophium brevis* does not have flat expanded first articles of the first antenna and *A. salmonis* usually has 14–16 articles in the flagellum, (though occasional specimens will have 11–12). In *A. brevis*, the males have about 11 articles in the flagellum of the first antenna. The uropods of *A. salmonis* and *A. brevis* are quite dissimilar. In *A. salmonis*, the peduncle of the first uropod is armed on the outside edge with three to six long, slender spines and at the distal edge with two to three short, blunt spines. *Americorophium brevis* has instead only eight short, blunt spines. The third uropods of *A. salmonis* have many more and longer setae than those of *A. brevis*. The telson shape and spination of the two species are also quite different (compare Figs. 4, *A. brevis*, and Fig. 5, *A. salmonis* in this guide).

Females: *A. salmonis* and *A. stimpsoni* females are very much alike, with no strong distinguishing characteristics, so the species should not be differentiated solely by female specimens. The only *Americorophium* female of this group to have the half-moon hook is *A. spinicorne*, so this species is easily distinguished from others. *Americorophium brevis* has three pairs of spines, as well as a spine on the gland cone, instead of having two single spines on the underside of the fourth article of the second antenna. The first antenna has eight joints in the flagellum, while that of *A. salmonis* has ten.

Ecological Information

Range: Type locality is Puget Sound, Washington (Bousfield and Hoover 1997). Known range along the west coast of North America includes Coos Bay to Puget Sound and Alaska (Barnard 1954).

Local Distribution: Local distribution in mudflats of South Slough as well as Cox Island (Siuslaw Estuary), Tillamook Bay, Sixes River, Ten Mile Creek and Columbia River (Forsberg et al. 1977).

Habitat: Members of the Corophiidae inhabit small U-shaped tubes in soft sediments, or on hard surfaces (Chapman 2007). Occurs in muddy habitats and sometimes with algae (e.g. *Ulva*). Especially abundant in brackish estuaries with a high degree of silt and mud (Raymond et al. 1985; Kozloff 1993). Comparisons of macrofaunal communities within and outside of *Dendraster excentricus* beds found *Americorophium* species to be more prevalent where sand dollars were not present (Smith 1981). Corophiid amphipods are frequently used in tests of sediment toxicity and/or water quality (e.g. fluoranthene, Swartz et al. 1990; ivermectin, Davies et al. 1998; sewage outfall, Arvai et al. 2002; and nonylphenol, Hecht et al. 2004).

Salinity:

Temperature:

Tidal Level:

Associates:

Abundance: Populations often very dense and easily observed or collected in the field. The abundance of *Americorophium* species was measured in the Campbell River Estuary and ranged from zero to ~15,000–31,000 per square meter in July (Raymond et al. 1985). Densities of *A. salmonis* in the Copper River

Delta, Alaska were as high as 7,000 per square meter in August (Powers et al. 2002).

Life-History Information

Reproduction: Development in most amphipods is direct, lacking a larval stage, and little is known about the reproduction and development in *A. salmonis*. Ovigerous *A. salmonis* females and young have been observed in October (Ten Mile Creek). Ovigerous *A. spinicorne* females have been observed in February, March, May and December (Eriksen 1968). In the European species, *Corophium volutator*, breeding occurs in February (over-wintering population) and again in July–August. Young remain in brood pouch four weeks and females produce up to four broods per year (Green 1968).

Larva: Since most amphipods develop directly, they lack a definite larval stage. Instead the young developmental stage resembles small adults (e.g. Fig. 39.1, Wolff 2014).

Juvenile:

Longevity:

Growth Rate: Amphipod growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. Ruppert et al. 2004).

Food: A detritivore, *A. salmonis* sorts material with filtering gnathopods. Abdominal appendages create a water current that is filtered by the fine hairs on the gnathopods, and the filtrate is then scraped off and ingested (Miller 1984; Taghon 1984; Kozloff 1993).

Predators: Young fish (e.g. Pacific Staghorn Sculpins, Starry Flounders, Threespine Stickleback, Signal Crayfish, Brenneis et al. 2011). *Americorophium salmonis* is a particularly important component of juvenile salmonid diet (e.g. Chinook, Forsberg et al. 1977; Bottom and Jones 1990) and White Sturgeon (*Acipenser transmontanus*, McCabe et al. 1993). Avery and Hawkinson (1992) also found that Gray Whale populations exhibited great feeding activity in areas with high density of corophid tube mats dominated by the species *A. spinicorne*, in northern California.

Behavior:

Bibliography

1. ARVAI, J. L., C. D. LEVINGS, P. J. HARRISON, and W. E. NEILL. 2002. Improvement of the sediment ecosystem following diversion of an intertidal sewage outfall at the Fraser River Estuary, Canada, with emphasis on *Corophium salmonis* (amphipoda). Marine Pollution Bulletin. 44:511-519.
2. AVERY, W. E., and C. HAWKINSON. 1992. Gray whale feeding in a northern California estuary. Northwest Science. 66:199-203.
3. BARNARD, J. L. 1954. Marine amphipoda of Oregon. Oregon State College, Corvallis.
4. BOTTOM, D. L., and K. K. JONES. 1990. Species composition, distribution, and invertebrate prey of fish assemblages in the Columbia River Estuary. Progress in Oceanography. 25:243-270.
5. BOUSFIELD, E. L., and P. M. HOOVER. 1997. The amphipod superfamily Corophioidea on the Pacific Coast of North America. Part 5. Family Corophiidae: Corophiinae, new subfamily. Systematics and distributional ecology. Amphipacifica. 2:67-139.
6. BRENNIS, V. E. F., A. SIH, and C. E. DE RIVERA. 2011. Integration of an invasive consumer into an estuarine food web: direct and indirect effects of the New Zealand mud snail. Oecologia. 167:169-179.
7. CHAPMAN, J. W. 2007. Amphipoda: Gammaridea, p. 545-556. In: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
8. DAVIES, I. M., P. A. GILLIBRAND, J. G. MCHENERY, and G. H. RAE. 1998. Environmental risk of ivermectin to sediment dwelling organisms. Aquaculture. 163:29-46.
9. ERIKSEN, C. H. 1968. Aspects of the limno-ecology of *Corophium spinicorne* (Stimpson) (Amphipoda) and *Gnorimosphaeroma oregonensis* (Dana) (Isopoda). Crustaceana. 14:1-12.
10. FORSBERG, B. O., J. A. JOHNSON, and S. I. KLUG. 1977. Identification, distribution and notes on food habits of fish and shellfish in Tillamook Bay, Oregon. Oregon Department of Fish and Wildlife, s.l.
11. GREEN, J. 1968. The Biology of estuarine animals. University of Washington Press, Seattle.
12. HECHT, S. A., J. S. GUNNARSSON, B. L. BOESE, J. O. LAMBERSON, C. SCHAFFNER, W. GIGER, and P. C. JEPSON. 2004. Influences of sedimentary organic matter quality on the bioaccumulation of 4-nonylphenol by estuarine amphipods. Environmental Toxicology and Chemistry. 23:865-873.
13. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
14. LESTER, G. T., and W. H. CLARK. 2002. Occurrence of *Corophium spinicorne* (Stimpson, 1857) (Amphipoda: Corophiidae) in Idaho, USA. Western North American Naturalist. 62:230-233.
15. MCCABE, G. T., R. L. EMMETT, and S. A. HINTON. 1993. Feeding ecology of juvenile white sturgeon *Nacipenser transmontanus* in the lower Columbia River. Northwest Science. 67:170-180.
16. MILLER, D. C. 1984. Mechanical post-capture particle selection by suspension feeding and deposit feeding corophim. Journal of Experimental Marine Biology and Ecology. 82:59-76.
17. POWERS, S. P., M. A. BISHOP, J. H. GRABOWSKI, and C. H. PETERSON. 2002. Intertidal benthic resources of the Copper River Delta, Alaska, USA. Journal of Sea Research. 47:13-23.
18. RAYMOND, B. A., M. M. WAYNE, and J. A. MORRISON. 1985. Vegetation, invertebrate distribution, and fish utilization of the Campbell River Estuary, British Columbia, Canada. Canadian Manuscript Report of Fisheries and Aquatic Sciences:1 -33.
19. RUPPERT, E.E., R.S. FOX, and R.D BARNES. 2004. Invertebrate

- zoology: a functional evolutionary approach, 7th Edition. Thomson Brooks/Cole, Belmont, CA.
20. SAKAMAKI, T., and J. S. RICHARDSON. 2009. Dietary responses of tidal flat macrobenthos to reduction of benthic microalgae: a test for potential use of allochthonous organic matter. *Marine Ecology Progress Series*. 386:107-113.
 21. SHOEMAKER, C. R. 1949. The amphipod genus *Corophium* on the west coast of America. *Journal of the Washington Academy of Sciences*. 89:66-82.
 22. SMITH, A. L. 1981. Comparison of macrofaunal invertebrates in sand dollar (*Dendraster excentricus*) beds and in adjacent areas free of sand dollars. *Marine Biology*. 65:191-198.
 23. SWARTZ, R. C., D. W. SCHULTS, T. H. DEWITT, G. R. DITSWORTH, and J. O. LAMBERSON. 1990. Toxicity of fluoranthene in sediment to marine amphipods: A test of the equilibrium partitioning approach to sediment quality criteria. *Environmental Toxicology and Chemistry*. 9:1071-1080.
 24. TAGHON, G. L. 1982. Optimal foraging by deposit feeding invertebrates: roles of particle size and organic coating. *Oecologia*. 52:295-304.
 25. WOLFF, C. 2014. Amphipoda, p. 206-209. *In: Atlas of crustacean larvae*. J.W. Martin., J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.

Updated 2015

Americorophium spinicorne

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Amphipoda, Gammaridea
Family: Corophiidae

Taxonomy: *Corophium spinicorne* was among the first corophiid amphipods described in North America by Stimpson 1857. It was transferred to the genus *Americorophium* in 1997 based on morphological characters (Bousfield and Hoover 1997) (see **Possible Misidentifications**). Not all researchers have followed this transition in other *Americorophium* species (e.g. Lester and Clark 2002; Sakamaki and Richardson 2009), but we follow the nomenclature used in other current local intertidal guides (Chapman 2007).

Description

Size: Largest species of *Americorophium* on the west coast with females 8–10 mm, in length (South Slough of Coos Bay) and males 6 mm in length (Shoemaker 1949).

Color: Clear, with dark brown markings on antennae and thoracic segments.

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six segments comprising three **pleonites** (together the pleosome), three **urosomites** (together the urosome), and finally a **telson** at the animal posterior (see Plate 254, Chapman 2007). In members of the genus *Americorophium*, the body is flattened dorso-ventrally and rarely exceeds 1 cm in total length (including antennae) in local specimens (see Fig 46, Kozloff 1993).

Cephalon:

Rostrum: Rounded in both sexes (Fig. 3b, 4), but male rostra are sometimes straight (Fig. 3a) (Shoemaker 1949).

Eyes:

Antenna 1: Reaching to the middle of the fifth segment of the second antenna.

Flagellum with 11 (female) or 14–16 joints (male). Female may have one to three spines on the first and second peduncular joints (Fig. 5).

Antenna 2: Long as or longer than body in males. Fourth joint with large distal half-moon tooth and no small accessory tooth. Fifth joint with distal spine and proximal spine, which is well within tooth when joint is flexed (Fig. 1). Females have similar toothed fourth joint (Fig. 5), with spines also on the fifth joint. The fifth joint has a proximal spine that opposes the large half-moon tooth when the joint is flexed. Both sexes have prominent gland cones on the second article (Figs. 1, 5), but that of the female is acute and curves forward sharply (Fig. 5).

Mouthparts:

Pereon:

Coxae: Setose lamellae (pairs of brood plates attached to bases of coxae) (Fig. 6) are present in females only. Do not confuse with fleshy gills that are present on both sexes.

Gnathopod 1:

Gnathopod 2: Filtering type, with fine long setae, present in both sexes, morphology as in other *Americorophium* species.

Pereopods 3 through 7:

Pleon:

Pleonites:

Urosomites: Urosome and third uropod morphology as in other *Americorophium* species (see *A. brevis*, Figs. 3, 4).

Epimera:

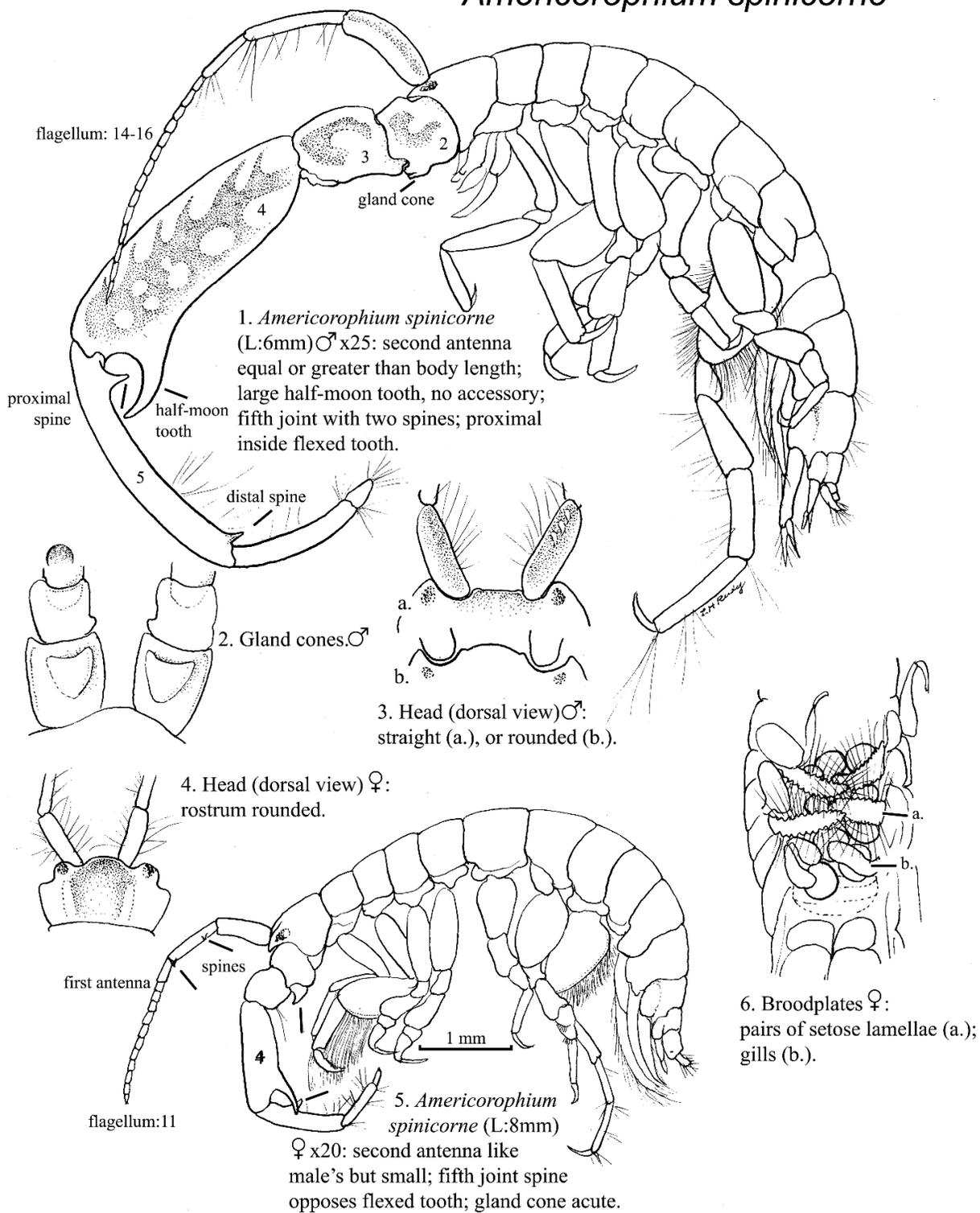
Telson:

Sexual Dimorphism: Sexes share a more similar morphology than other *Americorophium* species.

Possible Misidentifications

The gammarid family Corophiidae is characterized by individuals that build U-shaped tubes in both soft sediments and on hard surfaces, sometimes forming dense

Americorophium spinicorne



aggregations. Species can be dramatically sexually dimorphic and and, although males may be easier to identify with taxonomically relevant characters including the rostrum and peduncle of second antennae, most females can be reliably identified to species as well (Chapman 2007). Five corophiid genera occur locally, *Americorophium*, *Corophium*, *Crassicorophium*, *Laticorophium* and *Monocorophium*. The three common estuarine species in this guide (*A. brevis*, *A. salmonis*, *A. spinicorne*) were previously members of the genus *Corophium* (see Shoemaker 1949), but were transferred to the genus *Americorophium* in 1997 (Bousfield and Hoover 1997).

All *Americorophium* species have filtering-type second gnathopods and long setae on the third uropods. Of the four local *Americorophium* species, sexual dimorphism is strong in the three species *A. brevis*, *A. salmonis*, and *A. stimpsoni*. In particular, the second antenna and fourth segment differ between males and females (Shoemaker 1949). This is not the case, however, for the fourth *Americorophium* species, *A. spinicorne*, where male and female morphologies are similar. Additional characteristics that differ between species (particularly *A. brevis* and *A. salmonis*) include first antenna, telson, first uropods and third uropods.

Americorophium stimpsoni, principally a northern California species, does not seem to occur in Oregon. Its chief key characteristic is a prominent male rostrum, almost as long as the ocular lobes. The females are much like those of *A. salmonis*.

Americorophium spinicorne, another prominent northwest species, has less sexual dimorphism than other *Americorophium* species. Both males and females have a half-moon tooth on the fourth article of the second antenna, but without the small accessory tooth. *Americorophium spinicorne* is also strongly euryhaline and often found in fresh-water habitats. Segments of urosome are separate and not fused in *A. spinicorne* and males and females can be distinguished by the second antennal features (see **Antenna 2**) and by the presence of lamellae and/or eggs in females.

Males: Of the *Americorophium* species in which males have urosome segments dissimilar to females, *A. stimpsoni*, *A. brevis*, and *A. salmonis* all have a half-moon and accessory tooth on the fourth article of the second antenna. *Americorophium brevis* and *A. salmonis* often have similar rostrums, but that of *A. stimpsoni* has a prominent central lobe nearly as long as the ocular lobes. In *A. salmonis* the first antenna reaches only to the middle of the fourth article. *Americorophium brevis* does not have the flat expanded first articles of the first antenna and *A. salmonis* usually has 14–16 articles in the flagellum, (though occasional specimens will have 11–12). In *A. brevis*, the males have about 11 articles in the flagellum of the first antenna. The uropods of *A. salmonis* and *A. brevis* are quite dissimilar. In *A. salmonis*, the peduncle of the first uropod is armed on the outside edge with three to six long, slender spines and at the distal edge with two to three short, blunt spines. *Americorophium brevis* has instead only eight short, blunt spines. The third uropods of *A. salmonis* have many more and longer setae than those of *A. brevis*. The telson shape and spination of the two species are also quite different (compare Figs. 4, *A. brevis*, and Fig. 5, *A. salmonis* in this guide).

Females: *A. salmonis* and *A. stimpsoni* females are very much alike, with no strong distinguishing characteristics, so the species should not be differentiated solely by female specimens. The only *Americorophium* female of this group to have the half-moon hook is *A. spinicorne*, so this species is easily distinguished from others. *Americorophium brevis* has three pairs of spines, as well as a spine on the gland cone, instead of having two single spines on the underside of the fourth article of the second antenna. The first antenna has eight joints in the flagellum, while that of *A. salmonis* has ten.

Ecological Information

Range: Type locality is San Francisco, California (Bousfield and Hoover 1997). Known range includes estuaries and brackish waters from Santa Cruz, California to Alaska (Chapman 2007). Additionally, *A. spinicorne*

has been reported from two locations along the Snake River in Idaho (Lester and Clark 2002).

Local Distribution: Oregon estuaries and lakes including South Slough of Coos Bay, Tillamook Bay and Floras Lake.

Habitat: Members of the Corophiidae inhabit small U-shaped tubes in soft sediments, or on hard surfaces (Chapman 2007). Muddy substrates as well as sandy beaches (Barnard 1954), gravel and clay (Aldrich 1961). Individuals occur in areas of heavy silting (Kozloff 1993), but prefers sand (Eriksen 1968). Comparisons of macrofaunal communities within and outside of *Dendroaster excentricus* beds found *Americorophium* species to be more prevalent where sand dollars were not present (Smith 1981). Corophiid amphipods are frequently used in tests of sediment toxicity and/or water quality (e.g. fluoranthene, Swartz et al. 1990).

Salinity: Brackish to freshwater where salinities range from 0.02–33.6 (Eriksen 1968).

Temperature: 10–22.8°C (Eriksen 1968).

Tidal Level:

Associates:

Abundance: Populations often very dense and easily observed or collected in the field. The abundance of *Americorophium* species was measured in the Campbell River Estuary and ranged from zero to ~15,000–31,000 per square meter in July (Raymond et al. 1985). Abundances in excess of 100 individuals per square meter have also been documented (Eriksen 1968). *Americorophium spinicorne* is the dominant invertebrate in the river bottom of the San Joaquin river estuary (Aldrich 1961).

Life-History Information

Reproduction: Development in most amphipods is direct, lacking a larval stage, and little is known about the reproduction and development in *A. spinicorne*. Ovigerous females have been observed in February, March, May and December (Eriksen 1968). In the European species, *Corophium volutator*, breeding occurs in February (over-wintering population) and again in July–August. Young remain in brood pouch four weeks and females produce up to four broods per year (Green 1968).

Larva: Since most amphipods develop directly, they lack a definite larval stage.

Instead the young developmental stage resembles small adults (e.g. Fig. 39.1, Wolff 2014).

Juvenile:

Longevity:

Growth Rate: Amphipod growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individual will have soft shells as the cuticle gradually hardens (Ruppert et al. 2004).

Food: A detritivore, ingesting particulate organic matter (Sakamaki and Richardson 2009), *A. spinicorne* sorts material with filtering gnathopods. Abdominal appendages create a water current that is filtered by the fine hairs on the gnathopods, and the filtrate is then scraped off and ingested (Miller 1984; Kozloff 1993).

Predators: The tidewater goby, *Eucyclogobius newberryi* (Swenson and McCray 1996), young Chinook salmon (Forsberg et al. 1977; Busby and Barnhart 1995) and white sturgeon (*Acipenser transmontanus*, McCabe et al. 1993) all feed on *A. spinicorne*. Avery and Hawkinson (1992) also found that grey whale populations exhibited greater feeding activity in areas with high density of corophid tube mats and dominated by the species *A. spinicorne*, in northern California.

Behavior:

Bibliography

1. ALDRICH, F. A. 1961. Seasonal variations in the benthic invertebrate fauna of the San Joaquin River Estuary of California, with emphasis on the amphipod, *Corophium spinicorne* (Stimpson). Proceedings of the Academy of Natural Sciences of Philadelphia. 113:21-28.
2. AVERY, W. E., and C. HAWKINSON. 1992. Gray whale feeding in a northern California estuary. Northwest Science. 66:199-203.
3. BARNARD, J. L. 1954. Marine amphipoda of Oregon. Allan Hancock Foundation for Scientific Research. Contribution. 102.
4. BOUSFIELD, E. L., and P. M. HOOVER. 1997. The amphipod superfamily Corophioidea on the Pacific coast of North America. Part 5. Family Corophiidae: Corophiinae, new subfamily. Systematics and

- distributional ecology. *Amphipacifica*. 2:67-139.
5. BUSBY, M. S., and R. A. BARNHART. 1995. Potential food sources and feeding ecology of juvenile fall chinook salmon in California's Mattole River Lagoon. *California Fish and Game*. 81:133-146.
 6. CHAPMAN, J. W. 2007. Amphipoda: Gammaridea, p. 545-611. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 7. ERIKSEN, C. H. 1968. Aspects of the limno-ecology of *Corophium spinicorne* (Stimpson) (Amphipoda) and *Gnorimosphaeroma oregonensis* (Dana) (Isopoda). *Crustaceana*. 14:1-12.
 8. FORSBERG, B. O., J. A. JOHNSON, and S. I. KLUG. 1977. Identification, distribution and notes on food habits of fish and shellfish in Tillamook Bay, Oregon. Oregon Department of Fish and Wildlife, s.l.
 9. GREEN, J. 1968. The Biology of estuarine animals. University of Washington Press, Seattle.
 10. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
 11. LESTER, G. T., and W. H. CLARK. 2002. Occurrence of *Corophium spinicorne* (Stimpson, 1857) (Amphipoda: Corophiidae) in Idaho, USA. *Western North American Naturalist*. 62:230-233.
 12. MCCABE, G. T., R. L. EMMETT, and S. A. HINTON. 1993. Feeding ecology of juvenile white sturgeon *Nacipenser transmontanus* in the lower Columbia River. *Northwest Science*. 67:170-180.
 13. MILLER, D. C. 1984. Mechanical post-capture particle selection by suspension feeding and deposit feeding *Corophium*. *Journal of Experimental Marine Biology and Ecology*. 82:59-76.
 14. RAYMOND, B. A., M. M. WAYNE, and J. A. MORRISON. 1985. Vegetation, invertebrate distribution, and fish utilization of the Campbell River Estuary, British Columbia, Canada. Canadian Manuscript Report of Fisheries and Aquatic Sciences: 1-33.
 15. RUPPERT, E.E., R.S. FOX, and R.D. BARNES. 2004. Invertebrate zoology: a functional evolutionary approach, 7th Edition. Thomson Brooks/Cole, Belmont, CA.
 16. SAKAMAKI, T., and J. S. RICHARDSON. 2009. Dietary responses of tidal flat macrobenthos to reduction of benthic microalgae: a test for potential use of allochthonous organic matter. *Marine Ecology Progress Series*. 386:107-113.
 17. SHOEMAKER, C. R. 1949. The amphipod genus *Corophium* on the west coast of America. *Journal of the Washington Academy of Sciences*. 89:66-82.
 18. SMITH, A. L. 1981. Comparison of macrofaunal invertebrates in sand dollar (*Dendraster excentricus*) beds and in adjacent areas free of sand dollars. *Marine Biology*. 65:191-198.
 19. SWARTZ, R. C., D. W. SCHULTS, T. H. DEWITT, G. R. DITSWORTH, and J. O. LAMBERSON. 1990. Toxicity of fluoranthene in sediment to marine amphipods: a test of the equilibrium partitioning approach to sediment quality criteria. *Environmental Toxicology and Chemistry*. 9:1071-1080.
 20. SWENSON, R. O., and A. T. MCCRAY. 1996. Feeding ecology of the tidewater goby. *Transactions of the American Fisheries Society*. 125:956-970.
 21. WOLFF, C. 2014. Amphipoda, p. 206-209. *In: Atlas of crustacean larvae*. J.W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.

Updated 2015

Eohaustorius estuarius

A sand-burrowing amphipod

Phylum: Arthropoda, Crustacea
Subphylum: Malacostraca
Order: Amphipoda, Gammaridea
Family: Haustoriidae

Description

Size: Holotype is a female from Yaquina Bay, Oregon that is 4 mm in length. Paratypes are 2.0–4.5 mm in length (measured from the distal anterior end to the posterior telson) (Bosworth 1973). The illustrated specimens, collected from the lower Columbia River, were up to 6 mm long (Fig. 1).

Color: White, in life and in preservation (Bosworth 1973).

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) or cephalothorax includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six pairs of pleopods. The first three sets of pleopods are generally used for swimming, while the last three are simpler and surround the telson at the animal posterior. The amphipod family Haustoriidae are abundant in clean, fine sand in estuaries or marine habitats where they swim and burrow upside-down (Chapman 2007).

Cephalon:

Rostrum: Short, visor-like and pointed (Fig. 2).

Eyes: Visible in live specimens (not once preserved). Bright white in anterior distal corners of head (Bosworth 1973). Ovoid in shape, with irregular indentations, not protruding above the surface. Eyes probably not compound (Fig. 2).

Antenna 1: Massive, setose and not geniculate (i.e. bent like a knee) (Fig. 2).

Antenna 2: Peduncle articles large and flat, very setose and with multiarticulate accessory flagellum (Fig. 3).

Mouthparts: Mandible with palp and always consisting of three articles (Haustoriidae, Barnard 1969). Palp with smooth molar (Fig. 4).

Pereon:

Coxae: Coxal plates one and two small and hidden beneath three and four (Fig. 1). Coxal margins rounded and not pointed.

Gnathopod 1: Small, feeble and simple with article five longer than six (Kozloff 1987) (Fig. 1).

Gnathopod 2: Feeble, small and minutely chelate (Barnard 1969) (Fig. 5).

Pereopods 3 through 7: Pereopods lack dactyls (i.e. have only six articles), are furry and fringed with long bristles (*Eohaustorius*, Kozloff 1987). Pereopod four is smaller than pereopod three and is reversed and positioned like pereopods 5–7, not like 1–3 (Barnard 1969; 1975) (Fig. 1). Pereopod five with only one fascicle (bundle) of spines on posterior edge of article six and with articles five and six relatively equal in length (Bosworth 1973) (Fig. 1). Pereopod six like pereopod seven in length and general shape (i.e. not excessively long, Barnard 1975). Pereopod seven with posterior dorsal corner of article two smoothly rounded, without a cusp (arrow, Fig. 1) and with article five having two fascicles of spines on its anterior edge (Fig. 1).

Pleon:

Pleonites: Third pleonites with a fine posterior fringe (Fig. 1).

Urosomites: Segments two and three not fused, but freely articulated (Kozloff 1987). Urosomites small and hidden beneath pleonites (Figs. 1, 6). Third uropods each with two rami of equal length (Barnard 1969) (Fig. 7).

Epimera:

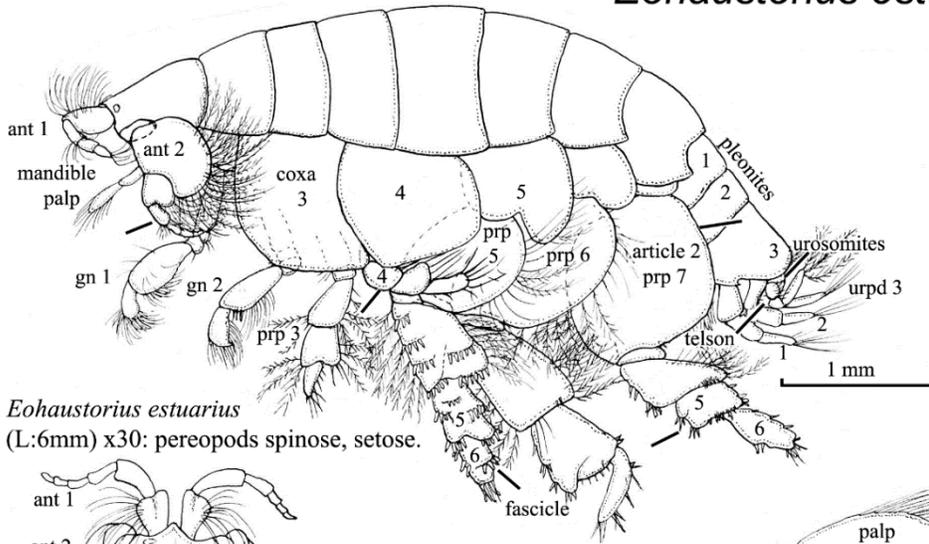
Telson: Thin, flattened, setose lobes that are widely separated at bases by urosomites (Haustoriidae, Barnard 1975) (Fig. 6).

Sexual Dimorphism: No obvious differences between males and females (Bosworth 1973).

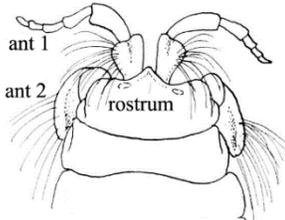
Possible Misidentifications

The Phoxocephalidae and Haustoriidae are morphologically similar gammarid amphipod families. Unlike the latter, Phoxocephalidae have very dissimilar pereopods six and seven: six is long and

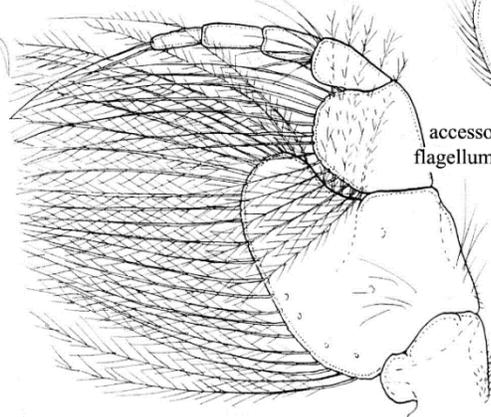
Eohaustorius estuarius



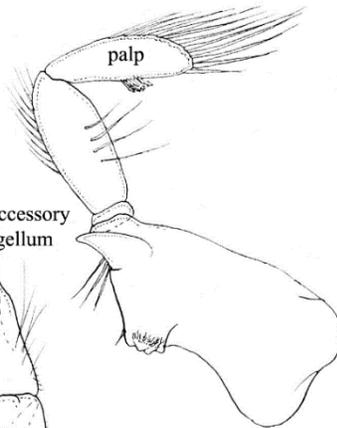
1. *Eohaustorius estuarius*
(L:6mm) x30: pereopods spinose, setose.



2. Anterior (dorsal view) x30.



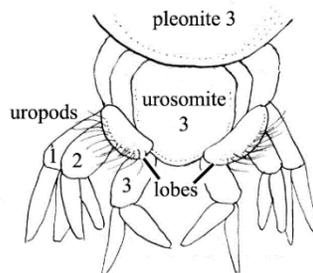
3. Antenna 2 x75: multiarticulate.



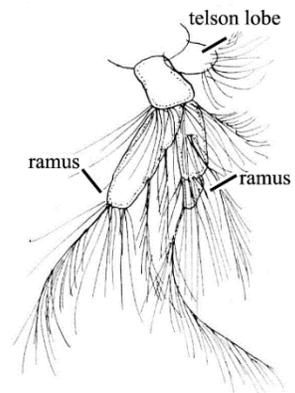
4. Left mandible x75.



5. Gnathopod 2 x75: dactyl minutely chelate.



6. Telson and uropods x30: telson lobes separated by urosomite; lobes setose.



7. Uropod 3 x75 two equal rami.

seven has a broad second article (see *Eobrolgus spinosus*). In the phoxocephalids, the fourth pereopod is not reversed as in the Haustoriidae, and although the rostrum is visor-like, it is much longer.

The Haustoriidae have feeble gnathopods, a mandible with a 3-articled palp, and spinose and setose pereopods. There are many genera in the family, but *Eohaustorius* is the only genus in which all the pereopods (3–7) lack dactyls (Barnard 1969). It is also the only genus of the family found in (and restricted to) the northern Pacific (Barnard 1969), where there are six species (Chapman 2007).

Eohaustorius is the only genus in the family Haustoriidae that occurs exclusively on Pacific coasts (from Russia to Mexico, Slattery 1985; Bousfield and Hoover 1995). Six species in the genus have been found in Oregon and four were described by Bosworth in 1973 (*Eohaustorius brevicuspis*, *E. sawyeri*, *E. washingtonianus* and *E. estuarius*). *Eohaustorius brevicuspis* and *E. sawyeri* inhabit only the open coast (Bosworth 1973). *Eohaustorius brevicuspis* was described from Lost Creek Beach, south of Newport, Oregon (Bosworth 1973). It has a small cusp on the dorsal posterior margin of article two of pereopod seven and it has only two fascicles of spines on the posterior edge of article six or pereopod seven. This species is found high in the intertidal, from +0.6 to 3.6 meters MLLW, and never in brackish water (Bosworth 1973). *Eohaustorius sawyeri*, often found with *E. brevicuspis*, lacks the cusp on the seventh pereopod and has instead a bulge on the posterior edge of the second article (of the seventh pereopod). The posterior edge of the sixth article of pereopod seven has four fascicles of spines. This species is subtidal, marine and found from MLLW down to -0.76 meters. It has not been found in estuarine conditions (Bosworth 1973). The species most likely to be confused with *E. estuarius*, and which is also found occasionally in the more marine portions of estuaries, is *E. washingtonianus*. Described from Puget Sound, it has also been found in Coos Bay, Yaquina Bay, and in the lower Columbia River. This species can be larger than *E. estuarius*, to 8 mm long (Kozloff 1993). It has a prominent crescent-shaped cusp on the dorsal posterior edge of article two of pereopod seven and there are three fascicles

of spines on the posterior edge of article six, pereopod five. In the Newport area (e.g. Yaquina Bay), it overlaps with *E. brevicuspis* intertidally, and with *E. sawyeri* subtidally, being found from -0.76 to +1.22 meters (Bosworth 1973). *Eohaustorius sencillus* has a first gnathopod with a sixth article that is swollen and has an apical spine. The seventh article on gnathopod one is quite long. This species lacks the cusp on article two of pereopod seven (as does *E. estuarius*). *Eohaustorius sencillus* is found commonly from Monterey Bay, California (Barnard 1962) to southern California. *Eohaustorius barnardi* is a subtidal species that occurs in fine sand, and is 5 mm in length (Chapman 2007).

Ecological Information

Range: Type locality is Yaquina Bay, OR (Bosworth 1973) and known range includes the entire northeastern Pacific (Chapman 2007).

Local Distribution: Local distribution at several Coos Bay sites, including the North Bend Airport extension site. Additional sites in Oregon include Yaquina Bay (near the Hatfield Marine Science Center) and lower Columbia River.

Habitat: Burrows in relatively clean, medium sized sand with a fairly high proportion of organic material. An estuarine species, it is found on open coast only where there is freshwater runoff (Bosworth 1973).

Eohaustorius estuarius is a common species used in toxicity testing (e.g. Kohn et al. 1994; Kravitz et al. 1999; Hecht and Boese 2002; Kuo et al. 2010; Greenstein et al. 2013; Ernst et al. 2014). It is the primary species used in the San Francisco Bay Estuary Regional Monitoring Program where it has been tested for sensitivity to a wide variety of toxins including copper, fluoranthene, chlorpyrifos, permethrin, bifenthrin and cypermethrin, the latter four toxins eliciting the most sensitive response (Anderson et al. 2008).

Eohaustorius estuarius also exhibited a dramatic, short-term population decline following exposure to carbaryl, an oyster farming pesticide (Dumbauld et al. 2001).

Salinity: Brackish water (e.g. salinity at type locality ranges from 1–25).

Temperature:

Tidal Level: Intertidal and subtidal (up to 7 meters deep, Bosworth 1973; Chapman 2007). Some small permanent populations

occur in high intertidal if freshwater stream runoff occurs (Bosworth 1973).

Associates: Does not overlap with habitats of other Oregon *Eohaustorius* species, where *E. estuarius* is found in brackish water, *E. brevicuspis* occurs mid-intertidally and *E. washingtonianus* and *E. sawyeri* are found in the lower intertidal (Bosworth 1973).

Abundance: Densest at intertidal heights (Bosworth 1973).

Life-History Information

Reproduction: Most amphipods have separate sexes with some sex determination correlated with environmental conditions (Straude 1987). Females brood embryos in an external thoracic chamber and create a water flow by moving their pleopods to irrigate embryos. Development within this brood chamber is direct and individuals hatch as juveniles that resemble small adults, with no larval stage. Little is known about the reproduction and development in *E. estuarius*, however Slattery (1985) followed the reproduction of the congener *E. sencillus* from Monterey Bay, California, where mating occurs in the fall and ovigerous females can be found year round, with peaks in winter months. Brood sizes range from 3–6 eggs and egg sizes within the brood are 430 µm and, upon hatching, are 800–900 µm (Slattery 1985).

Larva: Since most amphipods are direct developing, they lack a definite larval stage. Instead this young developmental stage resembles small adults (e.g. Fig. 39.1, Wolff 2014).

Juvenile: Sexual maturity is reached after 2–3 molts in local species of the families Haustoriidae (e.g. *E. sencillus*) and Phoxocephalidae (e.g. *Rhepoxynius fatigans*, *R. abronius*) (Slattery 1985).

Longevity: The longevity of *E. estuarius* is not directly known, but local species in the families Haustoriidae (e.g. *E. sencillus*) and Phoxocephalidae (e.g. *Rhepoxynius fatigans*, *R. abronius*) are on an annual cycle (Slattery 1985).

Growth Rate: Amphipod growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens (Ruppert et al. 2004).

Food:

Predators: Fish, shorebirds.

Behavior: Phoxocephalid and haustoriid species tend to be very mobile and efficient burrowers (Slattery 1985) and *E. estuarius* is a strong digger, with an impressive armament of spines and setae used for digging.

Bibliography

1. ANDERSON, B. S., S. LOWE, B. M. PHILLIPS, J. W. HUNT, J. VORHEES, S. CLARK, and R. S. TJEERDEMA. 2008. Relative sensitivities of toxicity test protocols with the amphipods *Eohaustorius estuarius* and *Ampelisca abdita*. *Ecotoxicology and Environmental Safety*. 69:24-31.
2. BARNARD, J. L. 1962. A new species of sand-burrowing Amphipoda from California. *Bulletin of the Southern California Academy of Sciences*. 61:249-252.
3. —. 1969. The Families and genera of marine Gammaridean Amphipoda, p. 535. *In: United States National Museum Bulletin*, Washington, DC.
4. —. 1975. Phylum Anthropoda: Crustacea, Amphipoda: Gammaridea, p. 313-366. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
5. BOSWORTH, W. S. J. 1973. Three new species of *Eohaustorius* (Amphipoda: Haustoriidae) from the Oregon coast. *Crustaceana*. 25:253-260.
6. BOUSFIELD, E. L., and P. HOOVER. 1995. The amphipod superfamily Pontoporeioidea on the Pacific coast of North America. 1. Family Haustoriidae. Genus *Eohaustorius* (J.L. Barnard): systematics and distributional ecology. *Amphipacifica*. 2:35-63.
7. CHAPMAN, J. W. 2007. Amphipoda: Gammaridea, p. 545-611. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
8. DUMBAULD, B. R., K. M. BROOKS, and M. H. POSEY. 2001. Response of an estuarine benthic community to

- application of the pesticide carbaryl and cultivation of pacific oysters (*Crassostrea gigas*) in Willapa Bay, Washington. *Marine Pollution Bulletin*. 42:826-844.
9. ERNST, W., K. DOE, A. COOK, L. BURRIDGE, B. LALONDE, P. JACKMAN, J. G. AUBE, and F. PAGE. 2014. Dispersion and toxicity to non-target crustaceans of azamethiphos and deltamethrin after sea lice treatments on farmed salmon, *Salmo solar*. *Aquaculture*. 424:104-112.
 10. GREENSTEIN, D., S. BAY, M. JACOB, C. BARTON, K. SAKAMOTO, D. YOUNG, K. RITTER, and K. SCHIFF. 2013. Regional assessment of marine and estuarine sediment toxicity in Southern California, USA. *Environmental Monitoring and Assessment*. 185:2055-2065.
 11. HECHT, S., and B. L. BOESE. 2002. Sensitivity of an infaunal amphipod, *Eohaustorius estuarius*, to acute waterborne exposures of 4-nonylphenol: evidence of a toxic hangover. *Environmental Toxicology and Chemistry*. 21:816-819.
 12. KOHN, N. P., J. Q. WORD, D. K. NIYOGI, L. T. ROSS, T. DILLON, and D. W. MOORE. 1994. Acute toxicity of ammonia to four species of marine amphipod. *Marine Environmental Research*. 38:1-15.
 13. KOZLOFF, E. N. 1987. *Marine invertebrates of the Pacific Northwest*. University of Washington Press, Seattle.
 14. —. 1993. *Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia*. University of Washington Press, Seattle, WA.
 15. KRAVITZ, M. J., J. O. LAMBERSON, S. P. FERRARO, R. C. SWARTZ, B. L. BOESE, and D. T. SPECHT. 1999. Avoidance response of the estuarine amphipod *Eohaustorius estuarius* to polycyclic aromatic hydrocarbon-contaminated, field-collected sediments. *Environmental Toxicology and Chemistry*. 18:1232-1235.
 16. KUO, J., C. BUDAY, G. VAN AGGELEN, M. G. IKONOMOU, and J. PASTERNAK. 2010. Acute toxicity of emamectin benzoate and its desmethyl metabolite to *Eohaustorius estuarius*. *Environmental Toxicology and Chemistry*. 29:1816-1820.
 17. RUPPERT, E.E., R.S. FOX, and R.D BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*, 7th Edition. Thomson Brooks/Cole, Belmont, CA.
 18. SLATTERY, P. N. 1985. Life histories of infaunal amphipods from subtidal sands of Monterey Bay, California. *Journal of Crustacean Biology*. 5:635-649.
 19. STRAUD, C. P. 1987. Phylum or Subphylum Crustacea, Class Malacostraca, Order Amphipoda, p. 424-431. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathman (ed.). University of Washington Press, Seattle, WA.
 20. WOLFF, C. 2014. Amphipoda, p. 206-209. *In: Atlas of crustacean larvae*. J.W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.

Updated 2015

Allorchestes angusta

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Amphipoda, Gammaridea
Family: Hyalellidae

Taxonomy: Although current intertidal guides (e.g. Chapman 2007) place *A. angusta* within the family Hyalellidae, Serejo (2004) proposes that this family be combined with the closely related family Hyalidae (Bousfield and Hendrycks 2002) based on a 43-character matrix (and including *A. angusta*) to form the resulting Dogielinotidae. Authors continue to synonymize *A. oculatus* and *A. angusta*, based on the ambiguous description of the former species, until further material can be examined (see Hendrycks and Bousfield 2001).

Description

Size: The illustrated male specimen is 6–8 mm in length (from South Slough of Coos Bay), but females tend to be smaller.

Color: Bright green with dark red eyes and spots, yellow-green antenna. Females are splotchy brown.

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) or cephalothorax includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six pairs of pleopods. The first three sets of pleopods are generally used for swimming, while the last three are simpler and surround the telson at the animal posterior. The genus *Allorchestes* is recognizable with a broad rectangular telson (Barnard 1974).

Cephalon:

Rostrum: Small and with lateral lobes that are broadly subtruncated (Barnard 1952)

Eyes: Eyes large, red and positioned antero-laterally (Fig. 1).

Antenna 1: Shorter than the second antenna in males (Fig. 1). The female's first antenna is subequal.

Antenna 2: Longer than first five body segments (Fig. 1) (Barnard 1952).

Mouthparts: Mandible with well developed rasping surface on molar, 2–3 spines, five teeth and no palps (Fig. 2). The tip of the inner plate of maxilliped with three stout spines, setae and article four developed (Fig. 4). First maxilla is with minute palp (Fig. 3) (Shoemaker 1941).

Pereon:

Coxae: Coxae 1–3 with posterior cusp, coxa four with lower convex margin, coxa five shallow. Gills are medium to large in size, sac-like, with the smallest at pereopod two. Coxal plates 2–4 are deep and broad in females (Hendrycks and Bousfield 2001).

Gnathopod 1: Stout. Article five is elongated (Fig. 1).

Gnathopod 2: Very large, article five elongated and article six is oval, tapering and with palm oblique. The dactyl is large, curved and fits the palm in males (Fig. 5). Article four larger than article three.

Pereopods 3 through 7: Pereopods three and four with short setae and pereopod five is longer than pereopod four.

Pleon:

Pleonites:

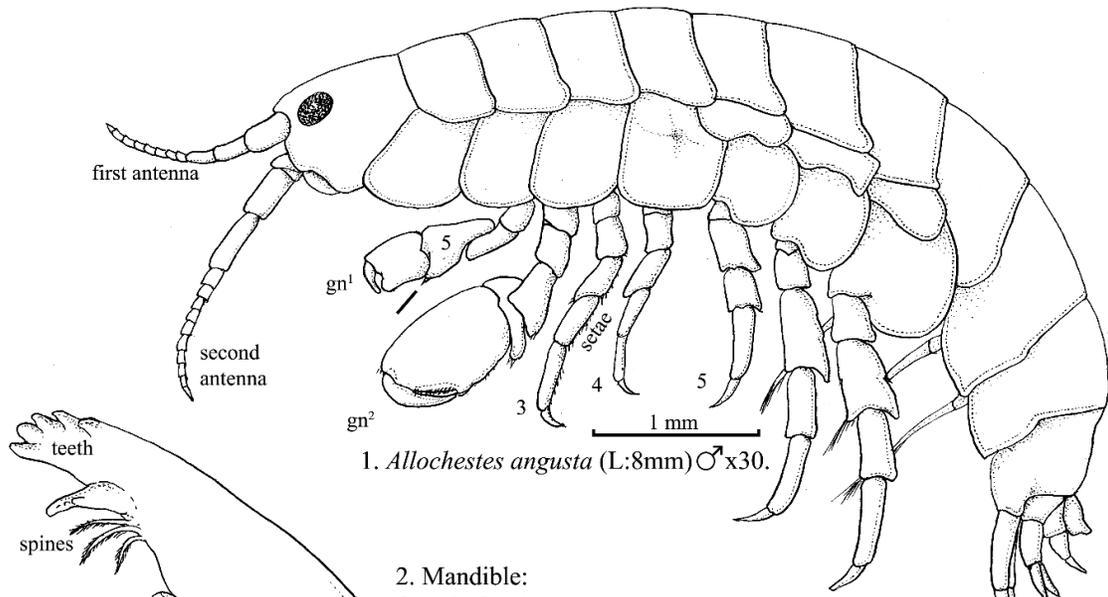
Urosomites: Uropod one and two without marginal spines on outer ramus (Hendrycks and Bousfield 2001). Third uropod with one small, flexible ramus and one spine (Fig. 6) (Barnard 1975).

Epimera: Plates two and three with posterior corners acute (Hendrycks and Bousfield 2001).

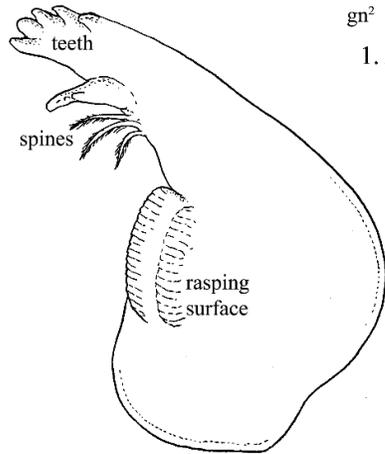
Telson: Rectangular and with cleft halfway. Telson compressed laterally in cross section (Fig. 7a, b) (Barnard 1975).

Sexual Dimorphism: Among amphipods, males generally have larger eyes, antennae and gnathopods (Straude 1987). Female *A. angusta* are smaller, have subequal antenna, first **gnathopod** palm that is transverse (not oblique) and second **gnathopod** slightly larger than the first (see Hendrycks and Bousfield 2001).

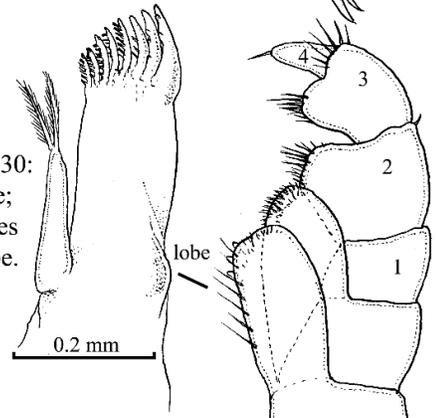
Allorchestes angusta



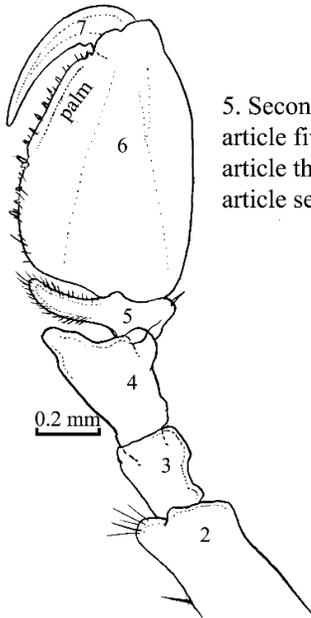
1. *Allorchestes angusta* (L:8mm) ♂ x30.



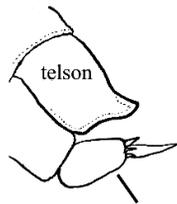
2. Mandible:
5 teeth, 3 spines
strong rasping surface,
no palp.



3. First maxilla x130:
inner plate: 2 setae;
outer plate: 3 spines
minute palp or lobe.



5. Second gnathopod ♂ x55:
article five produced;
article three short;
article seven curved.



6. Third uropod:
one ramus, flexible and
rudimentary; no minute
inner ramus.



7a. Urosome: cross-section
urosome compressed laterally.



b. Telson:
rectangular, cleft halfway.

4. Maxilliped:
article four developed
(from Hendrycks and Bousfield 2001).

Possible Misidentifications

The Hyalellidae are a family of gammarid amphipods characterized by highly modified first gnathopods in males and correspondingly modified ventral pereonites (pereonite two) and dorsal coxae (coxa two) in females. Four species occur locally, three of which are in the genus *Allorchestes*, which is characterized by a smooth posterior edge of pereopod seven, article two and a habitat that is primarily marine or estuarine. On the other hand, the local species *Hyaella azteca* is mostly found in freshwater and has a serrated posterior edge of pereopod seven on article two.

Allorchestes bellabella has an inflated dactyl on the first gnathopod (males). *Allorchestes rickeri* and *A. angusta* are the most similar species in this genus but can be differentiated by the fourth article of the fifth pereopod. In *A. angusta* the width of the fourth article is 1/2 the length, while in *A. rickeri* it is 2/3 the length. Furthermore, the female coxa two has a pre-amplexing notch that is obtuse in *A. angusta* and at a right angle in *A. rickeri* (see plate 272H and 272J in Chapman 2007).

Parallorchestes ochotensis, a similar species in the closely related family Hyalidae, does not have the produced article five on the second gnathopod, and has a small inner ramus on the third uropod. Furthermore, its telson has two triangular lobes.

Ecological Information

Range: Type locality is in California (Barnard 1974; Hendrycks and Bousfield 2001). Known Pacific range includes Japan to Laguna Beach, California, however *A. angusta* is rare south of Monterey (Barnard 1969).

Local Distribution: Coos Bay sites at North Bay of Cape Arago, Bay channel, South Slough and the Metcalf Preserve (Barnard 1969).

Habitat: Algae and eelgrass. Known substrates include mud, wood chips, coarse sand and cobble although individuals also occur in plankton samples (Barnard 1954). *Allorchestes angusta* was also found as a member of a phytal (drifting seaweeds)

community collected from northern Japan (Sano et al. 2003).

Salinity:

Temperature:

Tidal Level: High intermediate (Metcalf Preserve): + 0.6–1.2 meters (Yu et al. 2002).

Associates: Associate species include other tanaid amphipods (e.g. *Leptochelia*) and polychaetes.

Abundance: One of the common amphipods along the outer coast.

Life-History Information

Reproduction: Most amphipods have separate sexes with some sex determination correlated with environmental conditions (Straude 1987). Females brood embryos in an external thoracic brood chamber and irrigate embryos with a flow of water produced by pleopod movement. Development within this brood chamber is direct and individuals hatch as juveniles that resemble small adults, with no larval stage. Little is known about the development of *A. angusta*, however, an ovigerous female was found in July (Barnard 1954). The development of *Apoehyale pugettensis* (= *Hyale pugettensis*), a member of the Talitroidea superfamily and closely related family Hyalidae, is described and proceeds as follows: breeding in summer; individuals physically coupled for several days prior to copulation; brood sizes of 30 embryos; embryos 5–600 µm in diameter, hatching after 12 days at room temperature but remain within the female brood pouch for another 3–4 days (Straude 1987).

Larva: Since most amphipods are direct developing, they lack a definite larval stage. Instead, this young developmental stage resembles small adults (e.g. Fig. 39.1, Wolff 2014).

Juvenile:

Longevity:

Growth Rate: Amphipod growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens (Ruppert et al. 2004).

Food: Herbivore and detritivore (Yu et al. 2002; Chapman 2007).

Predators:

Behavior:

Bibliography

1. BARNARD, J. L. 1952. Some amphipoda from central California. *Wasmann Journal of Biology*. 10:20-23.
2. BARNARD, J. L. 1954. Marine amphipoda of Oregon. *Oregon State Monographs, Studies in Zoology*. No. 8:1-103.
3. BARNARD, J. L. 1969. Gammaridean amphipoda of the rocky intertidal of California: Monterey Bay to La Jolla. Smithsonian Institution Press, Washington.
4. BARNARD, J. L. 1974. Gammaridean amphipoda of Australia, Part. 2. *Smithsonian Contributions to Zoology*. No. 139:1-148.
5. BARNARD, J. L. 1975. Phylum Arthropoda: Crustacea, Amphipoda: Gammaridea, p. 313-366. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
6. BOUSFIELD, E. L., and E. A. HENDRYCKS. 2002. The Talitroidean amphipod family Hyalidae revised, with emphasis on the North Pacific fauna: Systematics and distributional ecology. *Amphipacifica*. 3:17-134.
7. CHAPMAN, J. W. 2007. Arthropoda: Amphipoda: Gammaridea, p. 545-618. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.).
8. HENDRYCKS, E. A., and E. L. BOUSFIELD. 2001. The amphipod genus *Allorchestes* in the north Pacific region: Systematics and distributional ecology. *Amphipacifica*. 3:3-37.
9. RUPPERT, E.E., R.S. FOX and R.D. BARNES. 2004. Invertebrate zoology: a functional evolutionary approach, 7TH Edition. Thomson Brooks/Cole, Belmont, CA.
10. SANO, M., M. OMORI, AND K. TANIGUCHI. 2003. Predator-prey systems of drifting seaweed communities off the Tohoku coast, northern Japan, as determined by feeding habit analysis of phytal animals. *Fisheries Science*. 69:260-268.
11. SEREJO, C. S. 2004. Cladistic revision of talitroidean amphipods (Crustacea, Gammaridea), with a proposal of a new classification. *Zoologica Scripta*. 33:551-586.
12. SHOEMAKER, C. R. 1941. On the names of certain California amphipods. *Proceedings of the Biological Society of Washington*. 54:187-188.
13. STRAUD, C. P. 1987. Phylum or Subphylum Crustacea, Class Malacostraca, Order Amphipoda, p. 424-431. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathman (ed.). University of Washington Press, Seattle, WA.
14. WOLFF, C. 2014. Amphipoda, p. 206-209. *In: Atlas of crustacean larvae*. J.W. Martin, J. Olesen, and J.T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
15. YU, O. H., H. Y. SOH, AND H. L. SUH. 2002. Seasonal zonation patterns of benthic amphipods in a sandy shore surf zone of Korea. *Journal of Crustacean Biology*. 22:459-466.

Updated 2015

Eobrolgus spinosus

A gammarid amphipod

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Amphipoda, Gammaridea
Family: Phoxocephalidae

Taxonomy: The genera *Eobrolgus* and *Foxiphalus* were designated in 1979 by Barnard and included species formerly in the genus *Paraphoxus*, including *E. spinosus* (e.g. *Paraphoxus spinosus*) (Barnard and Barnard 1982).

Description

Size: Individuals to 4.5 mm in length (Puget Sound, Barnard 1960). The largest Oregon specimens were 3.5 mm (Coos Bay) and 2.4 mm (Yaquina Bay) (Kemp et al. 1985). Oviparous females are not longer than 5 mm (Barnard 1975).

Color: White, with black eyes.

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) or cephalothorax includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six pairs of pleopods. The first three sets of pleopods are generally used for swimming, while the last three are simpler and surround the telson at the animal posterior. Members of the gammarid family Phoxocephalidae are referred to as "spiny heads" due to their shield-like pointed rostrums. They are also one of the most abundant and diverse groups of crustaceans in this size range (1–10 mm, Chapman 2007). Unlike many amphipod groups, taxonomic keys tend to favor female specimens in the Phoxocephalidae (Chapman 2007).

Cephalon: Head tapers evenly and is not abruptly narrowed (Fig. 2) with length about as long as pereonites one through three (Barnard 1975) (Fig. 1).

Rostrum: Rostrum well developed and not constricted (*Eobrolgus*, Barnard 1979) (Fig. 1).

Eyes: Large, black and about same size in females (Figs. 1, 2) and immature

males, but is much larger in mature males (not figured).

Antenna 1: Female first antenna equal in length to second antenna. Flagellum has about seven articles (Fig. 3a) and accessory flagellum (in both sexes) is with about five articles.

Antenna 2: The peduncle of the second antenna in females is with some heavy spines and setae (Fig. 3b). The flagellum has about seven slender articles, and is shorter than the peduncle (Barnard 1960). The male flagellum is longer than the body in mature males and can have sensory clubs on proximal flagellar articles and on fifth peduncle articles (not figured). Immature males have flagella a little longer than peduncle.

Mouthparts: Epistome (a part of the lip) is not produced into cusp (Fig. 1a) (Barnard 1960). The Phoxocephalidae is one of few groups in which epistome is of taxonomic importance. For a lateral view, push antennae and mandibular palps aside (Barnard 1960). Mandible with tri-articled palp, feeble molar and no large process. Right female mandible is with simple lacinia mobilis (Barnard and Barnard 1981) (Fig. 4). The first maxilla is with biarticulate palp and an outer plate with nine spines (Barnard and Barnard 1981). Maxilliped palp of article four is without large distal setae (not figured).

Pereon:

Coxae: Coxal plate one almost as large as two. The fourth coxa is broad and the fifth rounded (Fig. 1). Coxal margins bear simple setae.

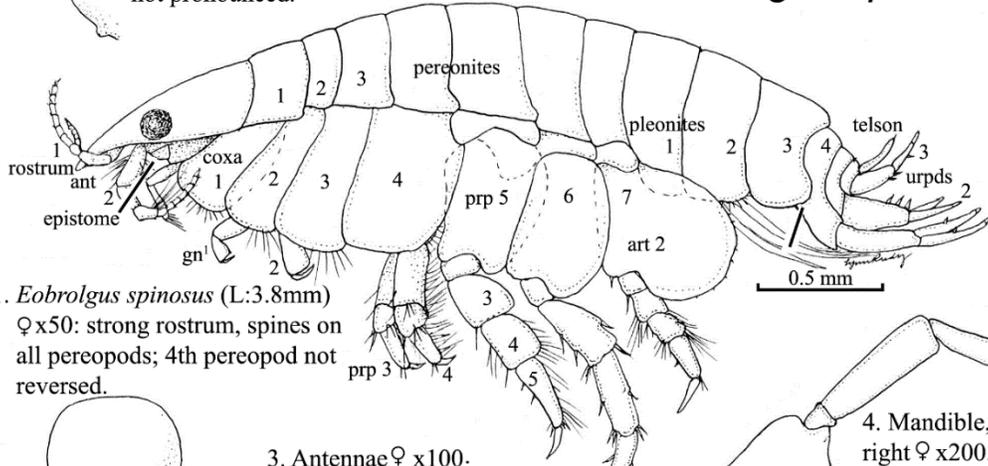
Gnathopod 1: Small. Similar in size and shape to the second gnathopods (*Eobrolgus*, Barnard 1979). Article six is broad.

Gnathopod 2: Much like first gnathopods. The first article is not pronounced (i.e. with even margins) and the sixth article is broad.

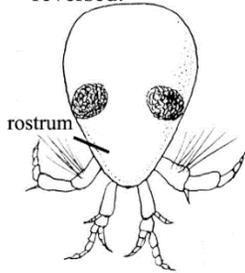
Pereopods 3 through 7: Pereopods with stout spines (Figs. 1, 6, 7). Pereopod four "normal" in orientation, not reversed like

Eobrolgus spinosus

1a. Epistome
not pronounced.

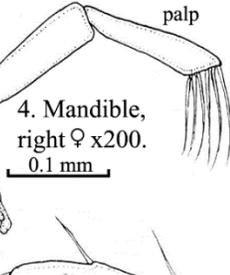
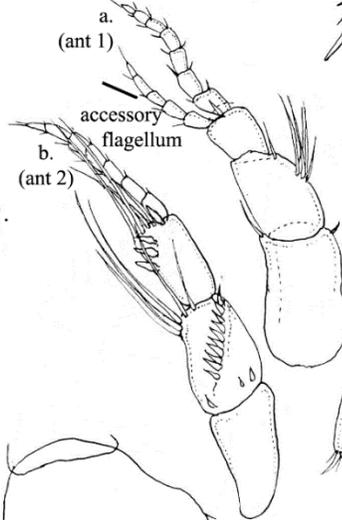



1. *Eobrolgus spinosus* (L:3.8mm)
♀ x50: strong rostrum, spines on all pereopods; 4th pereopod not reversed.

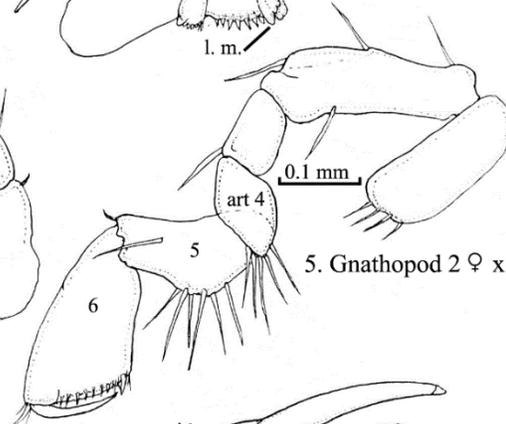


2. Head (dorsal view) ♀ x50.

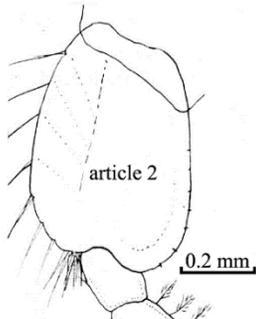
3. Antennae ♀ x100.



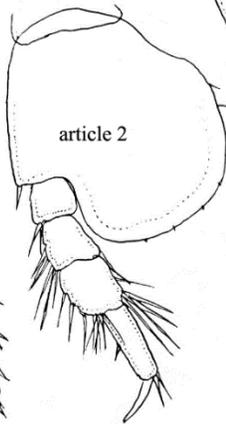
4. Mandible, right ♀ x200.
0.1 mm



5. Gnathopod 2 ♀ x160.

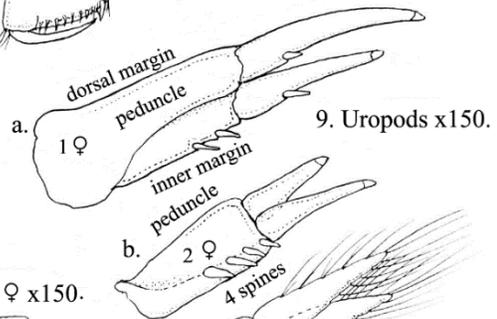
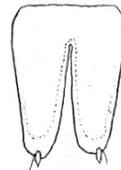


6. Pereopod 6 ♀ x75.

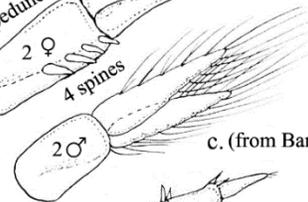


7. Pereopod 7 ♀ x75:
short, stout.

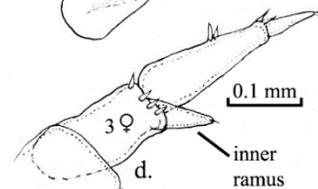
8. Telson ♀ x150.



9. Uropods x150.



c. (from Barnard, 1960)



0.1 mm

inner ramus

pereopods 5–7 (Barnard 1975) (see *Eohaustorius estuarius*). Pereopod five with second article broad, articles 4–5 expanded but narrower than article two (Fig. 1). Pereopod six is longer and more slender and with narrower article two than pereopod seven (Fig. 6). Pereopod seven is shorter, stouter and with article two broader than pereopod six and has rounded posterior edge with fine spines, no large spur (Fig. 7).

Pleon:

Pleonites: Fourth pleonite with proximal edge strongly depressed in males, while the edge is almost flush with segment three in females (*Eobrolgus*, Barnard 1960).

Urosomites: First urosomite peduncle with at least one dorsal margin, with only one or no spines and two spines on inner peduncle margin. Inner and outer branches similar, with one apical and one margin spine (Fig. 9a). Second uropods in females with four stout spines on peduncle margin, rami shorter than peduncle and without marginal spines (Fig. 9b) (Barnard 1960). In males, there are more spines on peduncle (not figured). The third uropods in females is with inner ramus half as long as (or slightly less than) outer (Fig. 9d). In males, the inner ramus is more than half as long as the outer and is quite setose in mature specimens (Fig. 9c) (Barnard 1960).

Epimera: The third epimeron is not produced into a tooth and is naked (i.e. bears no setae) (Barnard and Barnard 1981) (Fig. 1).

Telson: Telson, with cleft, is thin, lamellar and each lobe is with one short spine and one fine seta (Fig. 8).

Sexual Dimorphism: Not as strong as in some amphipod families. Males have larger eyes, much longer second antennae and spinose uropods (uropod three). Usual amphipod gnathopod sexual dimorphism is not observed in this genus (Barnard 1960; Chapman 2007).

Possible Misidentifications

Phoxocephalids can be distinguished primarily by their sixth and seventh pereopods, which are greatly different from each other. They also have distinctive multiarticulate accessory flagellae (on antenna one), and long rostrums (Barnard 1960). Hyalidae and Dogielinotidae are also estuarine families, but they lack mandibular

palps and inner rami on the third uropods. The Pleustidae have uncleft telsons and only vestigial antennal accessory flagella (Barnard 1975). Both the Gammaridae and Haustoriidae have pereopods that are similar in size and shape (not like the Phoxocephalidae) and in these families, pereopod four is reversed. Gammaridae have a telson with connected lobes (see *Eogammarus confervicolus*), while the telson lobes of Haustoriidae are disjunct (see *Eohaustorius estuarius*), and are much heavier than those of *Eobrolgus*.

The Phoxocephalidae is a diverse and abundant group of amphipods with 13 genera (comprising 30–45 species) represented locally including, *Mandibulophoxus* (one local species), *Cephalophoxoides* (one local species), *Heterophoxus*, (five local species), *Majoxiphalus* (one local species), *Metaphoxus* (one local species), and *Parametaphoxus* (one local species). Most phoxocephalid species formerly in *Paraphoxus* have been placed (by Barnard 1979) into one of six genera including *Metharpinia* (two local species), *Eyakia* (one local species), *Foxiphalus* (seven local species), *Grandifoxus* (three local species), *Rhepoxynius* (19 local species), and *Eobrolgus* (two local species).

Mandibulophoxus is distinguished from *Eobrolgus* by its sickle-shaped mandibular palp borne on a large process. It has a biarticulate palp on the first maxilla (like *Eobrolgus*). *Mandibulophoxus gilesi* is an eyeless, long-rostrumed species that has been found subtidally (to 14 meters depth) in Yaquina Bay and other Oregon estuaries (Chapman 2007).

Eobrolgus chumashi is an endemic oceanic species whose range probably extends only south of Oregon (Barnard and Barnard 1981). Its body is dwarfed and the head and eyes are large. The pleonal epimeron are not naked as in *E. spinosus*, but have 1–2 ventral setae. The lacinia mobilis (on the right mandible of the female) is bifid, not simple. Some hybridization between these two species of *Eobrolgus* may occur (Barnard and Barnard 1981; Chapman 2007).

The genera *Foxiphalus* and *Eobrolgus* are morphologically similar. Female *Eobrolgus* have a short second article on antenna one with a ventral surface that is continually covered with setae. Female

Foxiphalus, on the other hand, have a gap on the ventral side of antenna one. Confusingly, *Eobrolgus* males exhibit similar morphology of antenna one to *Foxiphalus* females and, thus, cannot be differentiated (Barnard and Barnard 1982) and, furthermore, *Foxiphalus* species are difficult to distinguish from *Majoxiphalus* (Chapman 2007). *Foxiphalus major* is probably the species most similar to *Eobrolgus spinosus*. Adults are larger than those of *E. spinosus* and ovigerous females are over 6 mm in length, but not under 5 mm. *Foxiphalus major* amphipods have longer heads and smaller eyes than do *E. spinosus* and their fifth pereopod is slender, not stout. The inner ramus of the female third uropod is more than ½ the length of the outer ramus (not less than ½, Fig. 9d). The third pleonal epimeron is concave or straight on its posterior edge and setose. *Foxiphalus major* was found under its old name (*Pontharpinia obtusidens*) on Oregon's outer coast (Barnard 1954, 1979).

Rhepoxynius tridentatus and others of this genus have an abruptly narrowing, untapered rostrum and the second article of pereopod seven has three large teeth on the posterior edge (Barnard 1954, 1979). *Rhepoxynius abronius*, with a broad head and narrow, short rostrum, has a long, sharp epistomal process. This species has large teeth on the posterior edge of pereopod seven. It has been reported from Yaquina Bay, Oregon.

Grandifoxus grandis (= *Grandifoxus milleri* and *Paraphosux milleri*) is found in the Columbia River estuary. This closely related species has a narrow gnathopod hand (sixth article) and an abruptly narrowing rostrum (Barnard 1960, 1979).

Ecological Information

Range: Type locality is New England (Homes 1905; Barnard and Barnard 1982). Known range includes the western Atlantic, from which it may have been introduced to the eastern Pacific. Distribution along the west coast of North America now includes Puget Sound, Washington to Newport Bay, California (Barnard and Barnard 1981).

Local Distribution: Coos Bay sites in South Slough, at Jordan Cove and at Pigeon Point (Barnard 1975). Other Oregon estuaries include Yaquina Bay.

Habitat: A burrower in sandy and muddy bottoms of estuaries that also tolerates substrates mixed with wood chips (e.g. Jordan Cove, Coos Bay). Phoxocephalid amphipods are sensitive to a variety of pollutants and are common subjects of toxicity tests (e.g. *Rhepoxynius abronius*, Robinson et al. 1988).

Salinity: Collected at salinities of 30 (Coos Bay).

Temperature:

Tidal Level: High and mid intertidal (Coos Bay) (Chapman 2007).

Associates: In beds of the ghost shrimp, *Neotrypaea*, and with the polychaetes, *Pygospio elegans* and *Pseudopolydora kempii*, outside of shrimp beds (Coos Bay, South Slough) (Posey 1985).

Abundance: Phoxocephalid amphipods are highly abundant, reaching densities up to 700 individuals per square meter in California (Oakden 1984). Dominant invertebrate at Jordan Cove, Coos Bay. Recorded June abundances: lower intertidal (+0.9 meters MLLW) 60–162 individuals per 13 x 15 cm core; mid intertidal (+1.0 meters MLLW) 92–174 individuals; high intertidal (+1.1 meters MLLW) 37–58 individuals (Posey 1985). Generally not as abundant as its close relative, *Foxiphalus major* (Barnard 1960).

Life-History Information

Reproduction: Most amphipods have separate sexes with some sex determination correlated with environmental conditions (Straude 1987). Females brood embryos in an external thoracic brood chamber and create a water flow by moving their pleopods to irrigate embryos. Development within this brood chamber is direct and individuals hatch as juveniles that resemble small adults, with no larval stage. Little is known about the reproduction and development of *E. spinosus*, but the development of another phoxocephalid species, *Rhepoxynius abronius*, has been described (Slattery 1985; Kemp et al. 1985) and proceeds with few, large eggs per brood (e.g. 5–12 eggs per brood, Slattery 1985 and 4–16, Kemp et al. 1985). Individuals of *R. abronius* breed in winter months and females are ovigerous in late winter and early spring in Monterey, California and beginning in October in Yaquina Bay, Oregon (Kemp et al. 1985). Egg size is approximately 460 µm and, upon

hatching, are approximately 1.0 mm (Slattery 1985).

Larva: Since most amphipods are direct developing, they lack a definite larval stage. Instead this young developmental stage resembles small adults (e.g. Fig. 39.1, Wolff 2014).

Juvenile: Sexual maturity is reached after 2–3 molts in the phoxocephalid species, *Rhepoxynius fatigans*, and *R. abronius* (Slattery 1985), which, in *R. abronius*, is when individuals are approximately 2.7 mm in length (Kemp et al. 1985).

Longevity: Up to one year (Slattery 1985; Chapman 2007).

Growth Rate: Amphipod growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens (Ruppert et al. 2004). Growth rate of *Rhepoxynius abronius* new recruits was 0.3 mm per month (Kemp et al. 1985).

Food: Many phoxocephalids are detritivores, but some are also predators of larval polychaetes, and their grazing may affect community structure (Kemp et al. 1985). *Eobrolgus spinosus* is a common predator of small meiofaunal invertebrate taxa (e.g. larval, juvenile and adult polychaetes, nematodes, Oliver et al. 1982; Oakden 1984; Chapman 2007).

Predators: Fish, shorebirds.

Behavior: Males positively phototropic and attracted to night light, a trait that may be correlated with very large eyes.

Bibliography

1. BARNARD, J. L. 1954. Marine amphipoda of Oregon. Oregon State Monographs, Studies in Zoology. No. 8:1-103.
2. —. 1960. The amphipod family Phoxocephalidae in the eastern Pacific ocean, with analyses of other species and notes for a revision of the family. Allan Hancock Pacific Expedition. 18:171-376.
3. —. 1975. Phylum Anthropoda: Crustacea, Amphipoda: Gammaridea, p. 313-366. *In:* Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
4. —. 1979. Revision of American species of the marine amphipod genus *Paraphoxus* (Gammaridea: Phoxocephalidae). Proceedings of the Biological Society of Washington. 92:368-379.
5. BARNARD, J. L., and C. M. BARNARD. 1981. The amphipod genera *Eobrolgus* and *Eyakia* (Crustacea: Phoxocephalidae) in the Pacific Ocean. Proceedings of the Biological Society of Washington. 94:295-313.
6. —. 1982. Revision of *Foxiphalus* and *Eubrolgus* (Crustacea: Amphipoda: Phoxocephalidae) from American oceans. Smithsonian Contributions to Zoology: I-IV, 1-35.
7. CHAPMAN, J. W. 2007. Amphipoda: Gammaridea, p. 545-611. *In:* The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
8. HOLMES, S. J. 1905. The amphipoda of southern New England. US Government Printing Office.
9. KEMP, P. F., F. A. COLE, and R. C. SWARTZ. 1985. Life history and productivity of the phoxocephalid amphipod *Rhepoxynius abronius* (Barnard). Journal of Crustacean Biology. 5:449-464.
10. OAKDEN, J. M. 1984. Feeding and substrate preference in five species of Phoxocephalid amphipods from central California. Journal of Crustacean Biology. 4:233-247.
11. OLIVER, J. S., J. M. OAKDEN, and P. N. SLATTERY. 1982. Phoxocephalid amphipod crustaceans as predators on larvae and juveniles in marine soft-bottom communities. Marine Ecology Progress Series. 7:179-184.
12. POSEY, M. H. 1985. The Effects upon the macrofaunal community of a dominant burrowing deposit feeder, *Callianassa californiensis*, and the role of predation in determining its intertidal distribution. Ph.D. University of Oregon.
13. ROBINSON, A. M., J. O. LAMBERSON, F. A. COLE, and R. C.

- SWARTZ. 1988. Effects of culture conditions on the sensitivity of a Phoxocephalid amphipod, *Rhepoxynius abronius*, to cadmium sediment. *Environmental Toxicology and Chemistry*. 7:953-959.
14. RUPPERT, E.E., R.S. FOX, and R.D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*, 7th Edition. Thomson Brooks/Cole, Belmont, CA.
 15. SLATTERY, P. N. 1985. Life histories of infaunal amphipods from subtidal sands of Monterey Bay, California. *Journal of Crustacean Biology*. 5:635-649.
 16. STRAUD, C. P. 1987. Phylum or Subphylum Crustacea, Class Malacostraca, Order Amphipoda, p. 424-431. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathman (ed.). University of Washington Press, Seattle, WA.
 17. WOLFF, C. 2014. Amphipoda, p. 206-209. *In: Atlas of crustacean larvae*. J.W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.

Updated 2015

Megalorchestia pugettensis

A beach hopper

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Amphipoda, Gammaridea
Family: Talitridae

Taxonomy: Some species of the genus *Megalorchestia*, including *M. pugettensis*, were originally described as members of *Orchestoidea* (e.g. *O. pugettensis*) (Bousfield 2007). These talitrid sand hoppers were divided into two groups: 4-dentate species from the southern hemisphere (*Orchestoidea*) and 5-dentate species from the northern hemisphere (*Megalorchestia*) by Brandt in 1851 (Bousfield 1982). *Megalorchestia* species-level designations are currently in need of further study as *M. columbiana* and *M. pugettensis* likely contain at least three species each (Bousfield 1982).

Description

Size: Individuals up to 18 mm in length, excluding antennae (Bowers 1964). The illustrated specimen (from Coos Bay) is 17 mm in length.

Color: White, usually with three spots on last three coxae. The color pattern is particularly useful in *Megalorchestia* species identification (see Fig. 3, Bowers 1963). In particular, there are distinctive antero-posterior markings on the last three thoracic segments in *M. pugettensis* (see Fig. 4B, Bowers 1963).

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) or cephalothorax includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six pairs of pleopods. The first three sets of pleopods are generally used for swimming, while the last three are simpler and surround the telson at the animal posterior. Talitrid amphipods are in the suborder Gammaridea, one of the largest groups of amphipods in marine and estuarine habitats. They have smooth bodies that are only slightly compressed, are commonly called beach hoppers and can be highly abundant on coastal beaches, particularly at night (Bousfield 2007). *Megalorchestia* species are

characterized by a short and stocky body, small eyes and short antennae (for key see Bousfield 1982).

Cephalon:

Rostrum: Rostrum rounded and simple.

Eyes: Eyes large and oval in shape (Fig. 1).

Antenna 1: Short and slightly shorter than the third article of second antenna, especially in males (Fig. 1) (Barnard 1975).

Antenna 2: Massive peduncle of three articles that are, together, longer than the flagellum, especially in males (Fig. 1) (Barnard 1975). Flagellum of about 20 articles.

Mouthparts: Mandible without palp (Talitridae) and maxilliped article four not well developed. (Mouthparts not figured, see *Traskorchestia traskiana* in this guide).

Pereon:

Coxae: The coxae, or first pereopod article, has first plate $\frac{1}{2}$ as large as second plate (Fig. 1).

Gnathopod 1: In both sexes, the first gnathopod is simple and not subchelate. The strong dactyl is adapted for digging (Fig. 2) (Barnard 1975). Translucent processes (“blisters”) are present on articles three and six.

Gnathopod 2: Large and subchelate in males (Figs. 1, 3) and simple in females (not figured, more like gnathopod one).

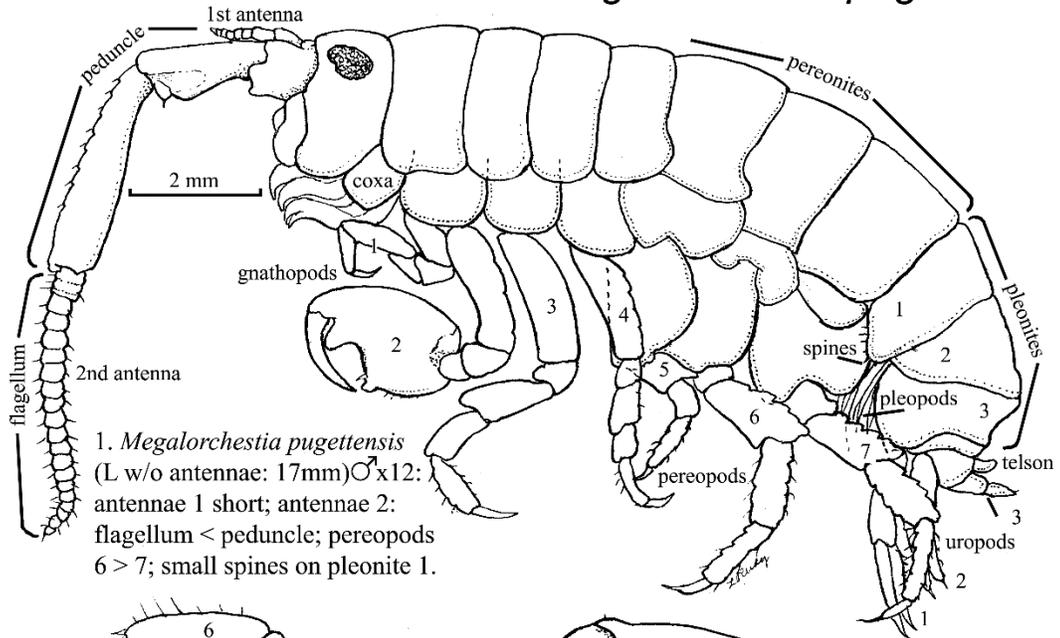
Pereopods 3 through 7: Pereopod six longer than seven (Fig. 1).

Pleon:

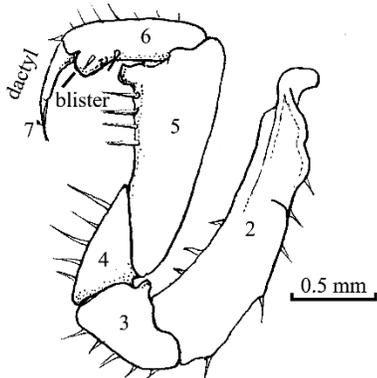
Pleonites: Pleonites five and six separate, not fused (Talitridae). Anteroventral margin of pleonite one is with 1–7 spines (Fig. 1). Three biramous pleopods (with small breathing organs within pleosome) and the third pleopod is about equal in size to first and second (not figured).

Urosomites: Three pairs of uropods: 1) outer branch with marginal spines (Fig. 4) and no interramal spine (not figured) and inner branch with double row of spines; 2) outer branch without spines on inner margin

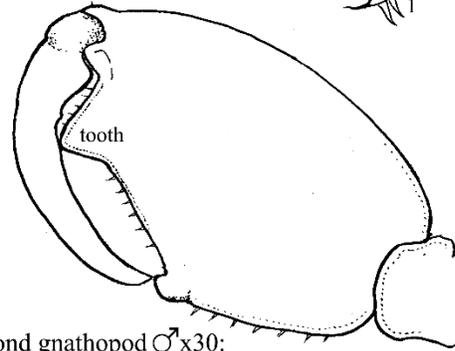
Megalorchestia pugettensis



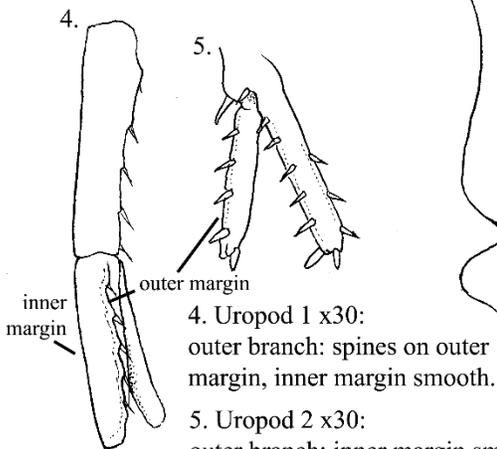
1. *Megalorchestia pugettensis*
(L w/o antennae: 17mm) ♂ x12:
antennae 1 short; antennae 2:
flagellum < peduncle; pereopods
6 > 7; small spines on pleonite 1.



2. First gnathopod ♂ x30:
dactyl simple, strong;
blister on article 6.

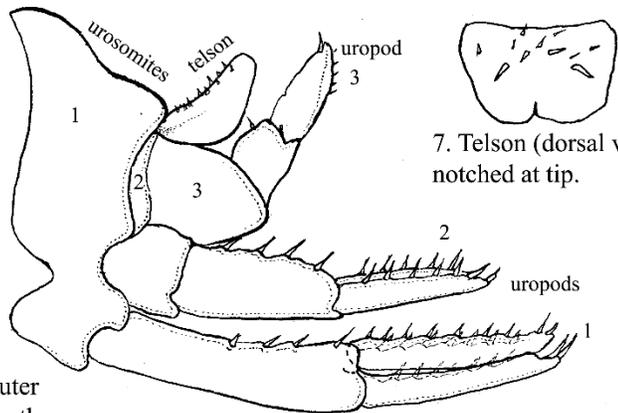


3. Second gnathopod ♂ x30:
chela large, powerful; tooth on palm.



4. Uropod 1 x30:
outer branch: spines on outer
margin, inner margin smooth.

5. Uropod 2 x30:
outer branch: inner margin smooth.



6. Urosome x30:
uropod 3: ramus broad, as long as peduncle.

7. Telson (dorsal view):
notched at tip.

(Figs. 5, 6); 3) one branch (Talitridae) and ramus broad distally and about as long as peduncle (Fig. 6) (Barnard 1975).

Epimera:

Telson: Telson spinose, notched at posterior-most tip (Figs. 1, 6, 7) and is often lost in collecting.

Sexual Dimorphism: Second gnathopods very large and powerful in males, but simple in females and young.

Possible Misidentifications

The Talitridae are a family of gammarid amphipods called beach hoppers and are ubiquitous in damp sands, where they live within clumps of seaweed. They survive well in air. Talitridae are characterized by a single branched third uropod (Figs. 1, 4) and a mandible without a palp (not figured, see *Traskorchestia traskiana* in this guide). Nine local talitrid species are currently reported (Bousfield 2007) including six *Megalorchestia*, two *Traskorchestia* and one *Transorchestia* species. Some authors differentiate *Megalorchestia* species as sand hoppers (intertidal on sandy beaches), while *Traskorchestia* species as beach fleas (intertidal in coastal leaf-litter) (Bousfield 1982; Pelletier et al. 2011).

The genus *Megalorchestia* are found on exposed beaches and are usually larger than *Traskorchestia*. Species in the latter genus have subchelate first gnathopods, not simple ones, and slender first gnathopod dactyls, not heavy ones. The seventh pereopods are also longer than the sixth, while the reverse is true in *Megalorchestia*. The third uropods narrows and branches in *Traskorchestia*, but is not broad.

Megalorchestia californiana, is the largest species in the Puget Sound area and (Kozloff 1974) is found on long stretches beaches with fine sand, high in the intertidal (Bowers 1963). It has a second antenna with a long flagellum (males), spines on the inner margin of the outer rami of the second uropod. The females have a translucent process on article five of the first gnathopod and the pleopod rami are short. Sexual dimorphism is strong in *M. californiana* and males have enlarged second gnathopods and elongated antennae with peduncle that is orange to red in color (Iyengar and Starks 2008). *Megalorchestia californiana* is often found with the smaller congener, *M.*

benedicti (Bousfield 2007). *Megalorchestia benedicti* is a small species (9–13 mm), and is found on fine sand beaches. Its pleonites have 1–5 spines on their posterior margins, making it potentially confused with *M. pugettensis*. Its telson is notched, however, and it lacks the characteristic translucent blister on the sixth article of the male gnathopod of *M. pugettensis*.

Megalorchestia corniculata, another large species, is found on short stretches of coarse sand beaches with lots of protection (Bowers 1963), seaweed and a steep slope. It has short second antennal flagella and spineless inner margins on the outer rami of its second uropods, like *M. pugettensis*. However, it has an entire, not a notched, telson, and no spines on the margin on its first pleonites. *Megalorchestia columbiana*, found on coarse sand beaches with little seaweed, has long second antennal flagella and no spines on the margins of its pleonites. Unlike *M. californiana*, it has no translucent process on female gnathopod one and its pleopod rami are ½ to ¾ the length of the peduncle. It can be as long as 22 mm (Bowers 1964). Finally, *M. minor* is a primarily southern species with distribution that is rarely north of San Simeon near Point Conception. Individuals are found on surf-exposed sandy beaches and are up to 15 mm in length (Bousfield 1982, 2007).

Ecological Information

Range: Information on the range of *M. pugettensis* is unknown outside the west coast of North America (e.g. central California to Alaska, Bousfield 1982, 2007).

Local Distribution: Coos Bay distribution in several locations along the South Slough and open coastal beaches.

Habitat: Under debris on coarse sand beaches with little seaweed (Barnard 1975). Sand hoppers (*Megalorchestia* species) are differentiated from beach fleas (*Traskorchestia* species) in that the former group tend to modify their habitat substrate, while the latter does not (Bousfield 1982).

Salinity:

Temperature:

Tidal Level: Above tide level, likes dampness, but avoids complete immersion in seawater.

Associates: Rhabditid nematodes are found under the dorsal pereonites in *M. californiana*

and *M. corniculata* (Rigby 1996). Talitrid amphipods also host and transport mites of Uropodina, Dermanyssina and Acaridida (Pugh et al. 1997).

Abundance: Not as common as *Traskorchestia traskiana* in Coos Bay.

Life-History Information

Reproduction: Most amphipods have separate sexes with some sex determination correlated with environmental conditions (Straude 1987). Females brood embryos in an external thoracic brood chamber and irrigate embryos with a flow of water produced by pleopod movement. Development within this brood chamber is direct and individuals hatch as juveniles that resemble small adults, with no larval stage. Little is known about the reproduction and development in *M. pugettensis*, but in congeners *M. californiana* and *M. corniculata*, pairing occurs in spring and young carried until they are 3 mm in length (Bowers 1964).

Larva: Since most amphipods are direct developing, they lack a definite larval stage. Instead this young developmental stage resembles small adults (e.g. Fig. 39.1, Wolff 2014).

Juvenile:

Longevity: The longevity of *M. pugettensis* is not known, but the possible life-span of the congener, *M. californiana* is two years maximum (Bowers 1964).

Growth Rate: Growth occurs in conjunction with molting. In the pre-molting period the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: Scavenges detritus from beach debris. The closely related *M. californiana* and *M. corniculata* are omnivorous, macrophagous, and partial to seaweed (e.g. *Macrocystis* and *Saccorhiza*, Lastra et al. 2008), wet cardboard and the bodies of other arthropods. However, individuals avoid putrefied matter.

Predators: Shorebirds and other birds (e.g. Varied Thrushes, *Ixoreus naevius*, Egger 1979). Talitrid amphipods are prey for a variety of intertidal and terrestrial predators and it has been suggested that they represent

a trophic link between the detritus of beach wrack and terrestrial ecosystems (via Pacific herring, Morritt and Spicer 1998; Fox et al. 2014).

Behavior: Many talitrid amphipods, including *M. pugettensis*, are nocturnal, potentially in an effort to avoid diurnal birds, for better moisture and temperature conditions for feeding, and because they are sensitive to light (Bowers 1964). The common term beach hopper comes from the ability of talitrid amphipods to jump using powerful extensor muscles and uropods (Bowers 1964; Iyengar and Starks 2008).

Bibliography

1. BARNARD, J. L. 1975. Phylum Anthropoda: Crustacea, Amphipoda: Gammaridea, p. 313-366. *In: Light's manual: intertidal invertebrates of the central California coast.* S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
2. BOUSFIELD, E. L. 1982. The Amphipod superfamily Talitroidea in the northeastern Pacific region. National Museums of Canada, Ottawa.
3. —. 2007. Talitridae, p. 611-618. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. T. Carlton (ed.). University of California Press, Berkeley, CA.
4. BOWERS, D. E. 1963. Field identification of five species of Californian beach hoppers (Crustacea: Amphipoda). *Pacific Science.* 17:315-320.
5. —. 1964. Natural history of two beach hoppers of the genus *Orchestoidea* (Crustacea: Amphipoda) with reference to their complemental distribution. *Ecology.* 45:677-696.
6. EGGER, M. 1979. Varied thrushes feeding on Talitrid amphipods. *Auk.* 96:805-806.
7. FOX, C. H., R. EL-SABAawi, P. C. PAQUET, and T. E. REIMCHEN. 2014. Pacific herring *Clupea pallasii* and wrack macrophytes subsidize semi-terrestrial detritivores. *Marine Ecology Progress Series.* 495:49-64.

8. IYENGAR, V. K., and B. D. STARKS. 2008. Sexual selection in harems: male competition plays a larger role than female choice in an amphipod. *Behavioral Ecology*. 19:642-649.
9. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
10. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
11. LASTRA, M., H. M. PAGE, J. E. DUGAN, D. M. HUBBARD, and I. F. RODIL. 2008. Processing of allochthonous macrophyte subsidies by sandy beach consumers: estimates of feeding rates and impacts on food resources. *Marine Biology*. 154:163-174.
12. MORRITT, D., and J. I. SPICER. 1998. The physiological ecology of talitrid amphipods: an update. *Canadian Journal of Zoology*. 76:1965-1982.
13. PELLETIER, A. J. D., D. E. JELINSKI, M. TREPLIN, and M. ZIMMER. 2011. Colonisation of beach-cast macrophyte wrack patches by talitrid amphipods: a primer. *Estuaries and Coasts*. 34:863-871.
14. PUGH, P. J. A., P. J. LLEWELLYN, K. ROBINSON, and S. E. SHACKLEY. 1997. The associations of phoretic mites (Acarina: Chelicerata) with sand-hoppers (Amphipoda: Crustacea) on the South Wales coast. *Journal of Zoology*. 243:305-318.
15. RIGBY, M. C. 1996. The epibionts of beach hoppers (Crustacea: Talitridae) of the North American Pacific coast. *Journal of Natural History*. 30:1329-1336.
16. STRAUDE, C. P. 1987. Phylum or subphylum Crustacea, class Malacostraca, order Amphipoda, p. 424-431. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
17. WOLFF, C. 2014. Amphipoda, p. 206-209. *In: Atlas of crustacean larvae*. M. J.W., J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.

Updated 2015

Traskorchestia traskiana

A beach hopper

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Amphipoda, Gammaridea
Family: Talitridae

Taxonomy: The genus *Traskorchestia* was designated in 1982 by Bousfield based on taxonomic characters and individuals collected from field expeditions in 1955 from Alaska to Baja, California (for characters see Figs. 1–3, 5, Bousfield 1982). Many *Traskorchestia* species, including *T. traskiana* (e.g. *O. traskiana*) were previously members of *Orchestia* (Bousfield 1982; Bousfield 2007).

Description

Size: The illustrated individual (from South Slough of Coos Bay) is 20 mm in length. Individuals can be 13 mm or a little more (Barnard 1975).

Color: Pale brown, orange antennae. Overall body color dull green or gray-brown with slightly blue legs (see Plate 19, Kozloff 1993) (Ricketts and Calvin 1971).

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) or cephalothorax includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six pairs of pleopods. The first three sets of pleopods are generally used for swimming, while the last three are simpler and surround the telson at the animal posterior. Talitrid amphipods are in the suborder Gammaridea, one of the largest groups of amphipods in marine and estuarine habitats. They have smooth bodies that are only slightly compressed, are commonly called beach hoppers and can be highly abundant on coastal beaches, particularly at night (Bousfield 2007). *Traskorchestia* species are characterized by smooth unmodified bodies, lateral eyes and their small to medium size (for key see Bousfield 1982).

Cephalon:

Rostrum: Rostrum simple (Fig. 1).

Eyes: Eyes large and oval in shape (Fig. 1).

Antenna 1: Very short, consisting of five articles (Fig. 1) (Stebbing 1906).

Antenna 2: Short, peduncle not thickened, flagellum with 16 articles (16 in males, 12 in females) (Stebbing 1906). Both first and second antennae are less massive than the beach hoppers found on the more open coast (e.g. *M. pugettensis* Ricketts and Calvin 1971).

Mouthparts: Mandible without palp (Fig. 2) (Talitridae) and maxilliped with four articles, although the fourth is not well developed (Fig. 4) (Barnard 1954).

Pereon:

Coxae: The plate of coxa one is about half as long as coxa two (Fig. 1).

Gnathopod 1: Dactyl of gnathopod one is slender and subchelate, especially in mature males, although not as simple as in *Megalorchestia* (see *M. pugettensis*). Translucent process on article four (Fig. 5).

Gnathopod 2: Smooth convex palm with no spine at hinge of articles six and seven (Fig. 6).

Pereopods 3 through 7: Pereopod seven longer than six (Barnard 1975).

Pleon: Pleopods strong, biramous with the first three about equal in size and branches with 7–10 segments (not figured) (Barnard 1975).

Pleonites: Pleonites five and six not fused (Fig. 1) (Barnard 1975).

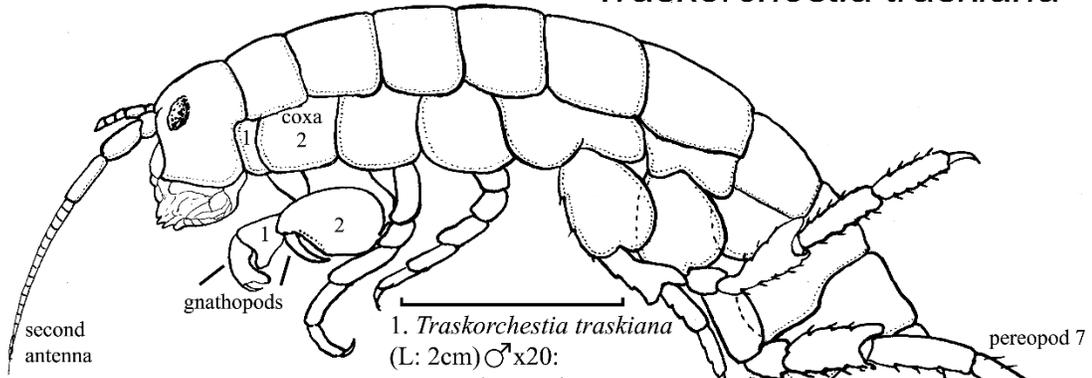
Urosomites: The third uropod is uniramous (Talitridae, Barnard 1954) with ramus shorter than peduncle and narrowing distally (Barnard 1975) (Fig. 3).

Epimera:

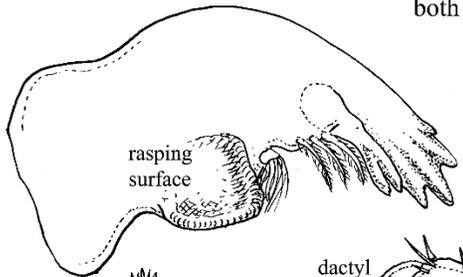
Telson: Telson puffy, split (not visible in lateral view) and with several spines (Fig. 3) (Barnard 1975).

Sexual Dimorphism: Males generally larger than females and with larger **gnathopods**. Populations in Washington state were dominated by females (63% compared to 37% male, Koch 1990).

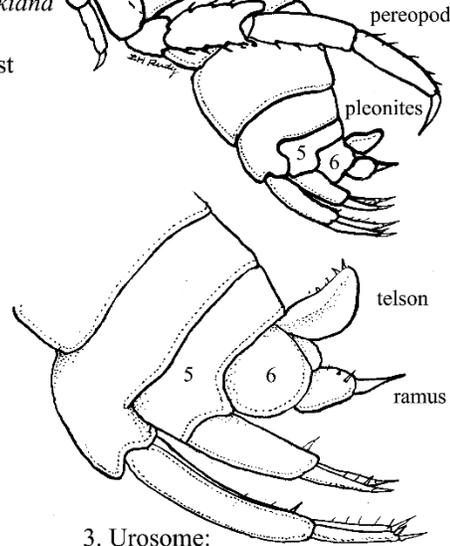
Traskorchestia traskiana



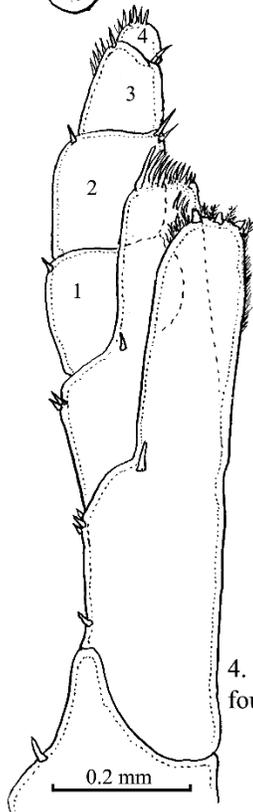
1. *Traskorchestia traskiana*
(L: 2cm) ♂x20:
pereopod seven longest
both antennae short.



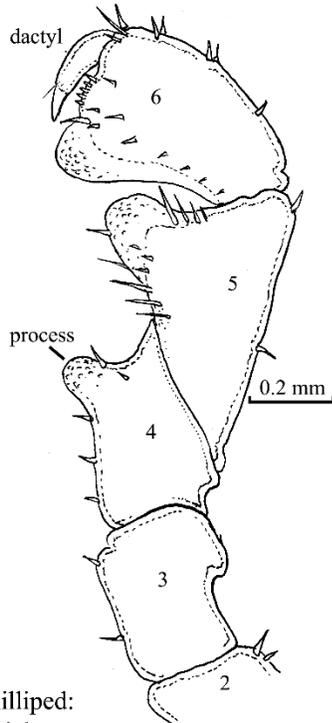
2. Mandible:
no palp.



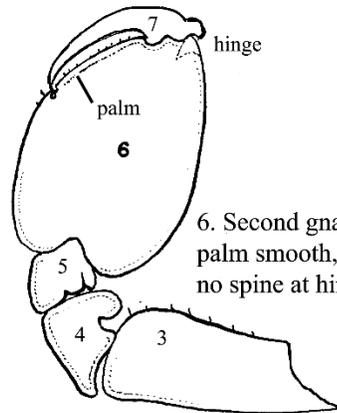
3. Urosome:
Telson: several spines, puffy;
third uropod:ramus narrowing,
shorter than peduncle.



4. Maxilliped:
four articles.



5. First gnathopod ♂:
subchelate, dactyl slender;
process on fourth segment.



6. Second gnathopod ♂:
palm smooth, convex;
no spine at hinge.

Possible Misidentifications

The Talitridae are a family of gammarid amphipods called beach hoppers and are ubiquitous in damp sands, where they live within clumps of seaweed. They survive well in air. Talitridae are characterized by a single branched third uropod (Figs. 1, 4 *Megalorchestia pugettensis*) and a mandible without a palp (Fig. 2). Nine local talitrid species are currently reported (Bousfield 2007) including six *Megalorchestia*, two *Traskorchestia* and one *Transorchestia* species. Some authors differentiate *Megalorchestia* species as sand hoppers (intertidal on sandy beaches), while *Traskorchestia* species as beach fleas (intertidal in coastal leaf-litter) (Bousfield 1982; Pelletier et al. 2011).

The genus *Megalorchestia* are found on exposed beaches and are usually larger than *Traskorchestia*. Species in the latter genus have subchelate first gnathopods, not simple ones, and slender first gnathopod dactyls, not heavy ones. The seventh pereopods are also longer than the sixth, while the reverse is true in *Megalorchestia*. The third uropods narrows and branches in *Traskorchestia*, but is not broad.

Traskorchestia species are larger than *Megalorchestia* and found on exposed beaches. *Traskorchestia georgiana* is up to 13.5 mm in length and is found with *T. traskiana* in the drift line on rocky beaches and amongst seagrass and algal debris. *Traskorchestia georgiana* has weak pleopods with 4–6 segments on the rami and its first gnathopod lacks the process on the fourth article (male) that is found on *T. traskiana* (Bousfield 1982).

Transorchestia enigmatica is another local talitrid amphipod species that is up to 15 mm in length. It was introduced in solid ballast from the southern hemisphere and is now found in Lake Merritt near San Francisco Bay, California (Bousfield and Carlton 1967). It is a member of the *T. chiliensis* species group, an introduced species found under debris on sandy beaches. *Transorchestia chiliensis* has a long, inflated second antenna and the second gnathopod has a sinuous dactyl and a triangular tooth near the hinge.

Ecological Information

Range: Type locality is in California (Bousfield 1982). Known range includes Aleutian Islands in Alaska to Washington state and south to Magdalena Bay, Baja California (Barnard 1954; Koch 1989b).

Local Distribution: Locally present at several locations in Coos Bay, at North Bay and Cape Arago (Barnard 1954).

Habitat: Rocky and/or sandy beaches with algae, salt marshes (under debris and boards) (Barnard 1975). Also occurs under driftwood on high protected beaches and inner *Salicornia* marshes (e.g. Metcalf Preserve) (Kozloff 1993). Beach fleas (*Traskorchestia* species) are differentiated from sand hoppers (*Megalorchestia* species) in that the former group tend not to modify their habitat substrate (Bousfield 1982).

Salinity: Euryhaline. Salinity tolerance ranges from brackish slough (Ricketts and Calvin 1971) to high beaches of salty bays (Kozloff 1993) and the outer coast (Barnard 1954). The majority of individuals tested (95%) survived for 24 hours in salinities ranging from 2.5 to 50 (Koch 1991).

Temperature: Up to 30–38°C (Morritt and Spicer 1998).

Tidal Level: Usually along the wrack line, but also found more than 20 meters above tidewater (Ricketts and Calvin 1971). A supralittoral species that can withstand desiccation of up to 25% of body water loss (Morritt and Spicer 1998), although desiccation resistance decreases in smaller individuals (Koch 1989b). Individuals prefer not to be inundated with water and will migrate upshore with an incoming tide (Koch 1989a).

Associates: In Metcalf Preserve, associates include other amphipods, sphaeromid isopods and the gastropod, *Ovatella*. Talitrid amphipods are known to host rhabditid nematodes under their dorsal pereonites (e.g. *Megalorchestia californiana* and *M. corniculata*, Rigby 1996) as well as within the intersegmental spaces in *T. traskiana* (Adamson and Rigby 1996). Talitrid amphipods also host and transport mites of Uropodina, Dermanyssina and Acaridida (Pugh et al. 1997) and an additional 12 mite species in the genus *Traskorchestianoetus* were reported from *Traskorchestia traskiana* in Vancouver Island, Canada (Fain and Colloff 1990). Black gill syndrome (BGS) is

found in many decapod crustaceans and has been reported for *Traskorchestia traskiana*. It can be caused by a variety of things including bacterial, fungal or protozoan infections. BGS causes darkening and, ultimately, loss of gills which results in a reduction of oxygen uptake (Spicer 2013). Spicer (2013) found that the osmoregulatory ability of high-shore individuals was most negatively affected by BGS, suggesting this syndrome could reduce the number of *T. traskiana* in upper intertidal and brackish waters (Spicer 2013).

Abundance: Often observed by the hundreds under debris. Individuals can reach densities of 55 individuals per gram of dry wrack (Koch 1989b).

Life-History Information

Reproduction: Most amphipods have separate sexes with some sex determination correlated with environmental conditions (Straude 1987). Females brood embryos in an external thoracic brood chamber and irrigate embryos with a flow of water produced by pleopod movement. Development within this brood chamber is direct and individuals hatch as juveniles that resemble small adults, with no larval stage. Little is known about the reproduction and development in *T. traskiana*, but some ovigerous females were observed in March in Coos Bay and reported during spring and summer in northern populations, where females produce two broods per year (e.g. Alaska, Koch 1990). Breeding occurred in February in Washington state and continued through spring (see Fig. 1, Koch 1990) and brood sizes ranged between six and 16 individuals per brood (Koch 1990).

Larva: Since most amphipods are direct developing, they lack a definite larval stage. Instead, this young developmental stage resembles small adults (e.g. Fig. 39.1, Wolff 2014).

Juvenile: Sexual dimorphism develops once individuals are longer than 6 mm (Koch 1990).

Longevity:

Growth Rate: Amphipod growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007). Growth in *T. traskiana* proceeds as one

podomere (leg bearing segment) per molt for up to 13 and 16 podomeres in females and males, respectively. Growth of antennal segments is positively correlated with overall body size (Page 1979).

Food: Scavenges in debris for detritus and tends to prefer aged and decomposing seaweeds in the wrack line (e.g. *Salicornia*, Page 1997) to fresh algae (Pennings et al. 2000).

Predators: Talitrid amphipods are prey for a variety of intertidal and terrestrial predators and it is suggested that they represent a trophic link between the detritus of beach wrack and terrestrial ecosystems (via fish predation Koch 1989a; Morritt and Spicer 1998; Fox et al. 2014). Other predators include shorebirds (e.g. seagulls, Koch 1989a) and other birds (e.g. Varied Thrushes, *Ixoreus naevius*, Egger 1979) and the nemertean, *Pantionemertes californiensis* (Roe 1993).

Behavior: Many talitrid amphipods, including *T. traskiana*, are probably completely nocturnal (Koch 1989b). *Traskorchestia traskiana* tend to migrate vertically along beaches, but rarely move laterally (Koch 1989a) and seek out beach wrack with olfactory cues (Pelletier et al. 2011).

Bibliography

1. ADAMSON, M. L., and M. RIGBY. 1996. Rhabditis (Crustorhabditis) stasileonovi (Belogurov) from beach hoppers (Talitridae; Amphipoda) from the Pacific coast of North America. *Fundamental and Applied Nematology*. 19:579-584.
2. BARNARD, J. L. 1954. Marine amphipoda of Oregon. Oregon State College, Corvallis, OR.
3. —. 1975. Phylum Anthropoda: Crustacea, Amphipoda: Gammaridea, p. 313-366. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
4. BOUSFIELD, E. L. 1982. The amphipod superfamily Talitroidea in the northeastern Pacific region 1. *Familie Tallitridae systematics and distributional ecology*. National

- Museum of Natural Sciences (Ottawa) Publications in Biological Oceanography: I-VIII, 1-73.
5. —. 2007. Talitridae, p. 611-618. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 6. BOUSFIELD, E. L., and J. T. CARLTON. 1967. New records of Talitridae (Crustacea: Amphipoda) from the central Californian coast. *Bulletin of the Southern California Academy of Science*. 66:277-284.
 7. EGGER, M. 1979. Varied thrushes feeding on Talitrid amphipods. *Auk*. 96:805-806.
 8. FAIN, A., and M. J. COLLOFF. 1990. A new genus and two new species of mites (Acari: Histiostomatidae) phoretic on *Traskorchestia traskiana* (Stimpson, 1857) (Crustacea: Amphipoda) from Canada. *Journal of Natural History*. 24:667-672.
 9. FOX, C. H., R. EL-SABA AWI, P. C. PAQUET, and T. E. REIMCHEN. 2014. Pacific herring *Clupea pallasii* and wrack macrophytes subsidize semi-terrestrial detritivores. *Marine Ecology Progress Series*. 495:49-64.
 10. KOCH, H. 1989a. Desiccation resistance of the supralittoral amphipod *Traskorchestia traskiana* (Stimpson, 1857). *Crustaceana*. 56:162-175.
 11. —. 1989b. The effect of tidal inundation on the activity and behavior of the supralittoral talitrid amphipod *Traskorchestia traskiana* (Stimpson, 1857). *Crustaceana*. 57:295-303.
 12. —. 1990. Aspects of the populations biology of *Traskorchestia traskiana* (Stimpson, 1857) (Amiphoda: Talitridae) in the Pacific Northwest, USA. *Crustaceana*. 59:35-52.
 13. —. 1991. Salinity tolerance and osmoregulation of *Traskorchestia traskiana* (Stimpson, 1857) (Amphipoda: Talitridae). *Crustaceana*. 61:21-37.
 14. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 15. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 16. MORRITT, D., and J. I. SPICER. 1998. The physiological ecology of talitrid amphipods: an update. *Canadian Journal of Zoology*. 76:1965-1982.
 17. PAGE, H. M. 1979. Relationship between growth, size, molting, and number of antennal segments in *Orchestia traskiana* (Stimpson) (Amphipoda: Talitridae). *Crustaceana*. 37:247-252.
 18. —. 1997. Importance of vascular plant and algal production to macro-invertebrate consumers in a southern California salt marsh. *Estuarine Coastal and Shelf Science*. 45:823-834.
 19. PELLETIER, A. J. D., D. E. JELINSKI, M. TREPLIN, and M. ZIMMER. 2011. Colonisation of beach-cast macrophyte wrack patches by talitrid amphipods: a primer. *Estuaries and Coasts*. 34:863-871.
 20. PENNING, S. C., T. H. CAREFOOT, M. ZIMMER, J. P. DANKO, and A. ZIEGLER. 2000. Feeding preferences of supralittoral isopods and amphipods. *Canadian Journal of Zoology*. 78:1918-1929.
 21. PUGH, P. J. A., P. J. LLEWELLYN, K. ROBINSON, and S. E. SHACKLEY. 1997. The associations of phoretic mites (Acarina: Chelicerata) with sand-hoppers (Amphipoda: Crustacea) on the South Wales coast. *Journal of Zoology*. 243:305-318.
 22. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 23. RIGBY, M. C. 1996. The epibionts of beach hoppers (Crustacea: Talitridae) of the North American Pacific coast. *Journal of Natural History*. 30:1329-1336.
 24. ROE, P. 1993. Aspects of the biology of *Pantionemertes californiensis*, a

- high intertidal nemertean.
Hydrobiologia. 266:29-44.
25. SPICER, J. I. 2013. Physiological changes accompanying the presence of black gill syndrome in the high shore amphipod *Traskorchestia traskiana*. *Journal of Experimental Marine Biology and Ecology*. 446:131-138.
 26. STEBBING, T. R. R. 1906. Amphipoda: Gammaridea. *Das Tierreich*. 21:1-806.
 27. STRAUDE, C. P. 1987. Phylum or subphylum Crustacea, class Malacostraca, order Amphipoda, p. 424-431. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 28. WOLFF, C. 2014. Amphipoda, p. 206-209. *In: Atlas of crustacean larvae*. M. J.W., J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.

Updated 2015

Caprella drepanochir

A skeleton shrimp, or caprellid amphipod

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Amphipoda, Caprellidea
Family: Caprellidae

Taxonomy: The Caprellidae are a very distinctive family of amphipods. They were previously a separate amphipod suborder, but were recently found to be polyphyletic, arising at least twice from different gammarid amphipod lineages (Laubitz 1993; Takeychi 1993; Watling and Carlton 2007). Current research places them as highly modified members of the suborder Corophiidea (Myers and Lowry 2003; Watling and Carlton 2007), a taxon divided into two infraorders (Caprellida, Corophiida) each with different evolutionary feeding strategies and associated morphology (Myers and Lowry 2003).

Descripton

Size: The illustrated specimens (from Coos Bay) include a 13 mm long male (Fig. 1) and an 8 mm long female (Fig. 2) (Measured from anterior (head) to posterior (abdomen), Laubitz 1970). Males collected in Japan were 13 mm (Arimoto et al. 1976; Utinomi 1943) while those from Alaska were 12.4 mm in length (Laubitz 1970).

Color: White, with brown chromatophores. The illustrated female is darker than the male specimen.

General Morphology: The body of amphipod crustaceans can be divided into three major regions. The **cephalon** (head) or cephalothorax includes antennules, antennae, mandibles, maxillae and maxillipeds (collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax) with seven pairs of pereopods attached to pereonites followed by the **pleon** (abdomen) with six pairs of pleopods. The first three sets of pleopods are generally used for swimming, while the last three are simpler and surround the telson at the animal posterior. Caprellid amphipods differ from the rest of amphipoda in that the abdomen is greatly reduced, especially the last three abdominal segments (urosome) and associated appendages (uropods). Their body is also elongated rather than laterally compressed (compare to gammarid amphipods, e.g. *Eogammarus*

confervicolus) (Kozloff 1993; Watling and Carlton 2007).

Cephalon: Round cephalon with no dorsal spines or tubercles (Fig. 1) (Laubitz 1976), however body spination is a highly variable trait among individuals (Watling and Carlton 2007). Head partially fused with the first pereonite (segment of pereon) and the first pair of gnathopods (Fig. 1). Pereonite one not more than twice as long as head in male (Laubitz 1970) and shorter in female (Laubitz 1970) (Fig. 2).

Rostrum: Cephalon without rostrum (Laubitz 1976).

Eyes: Small (Laubitz 1976) (Fig. 1).

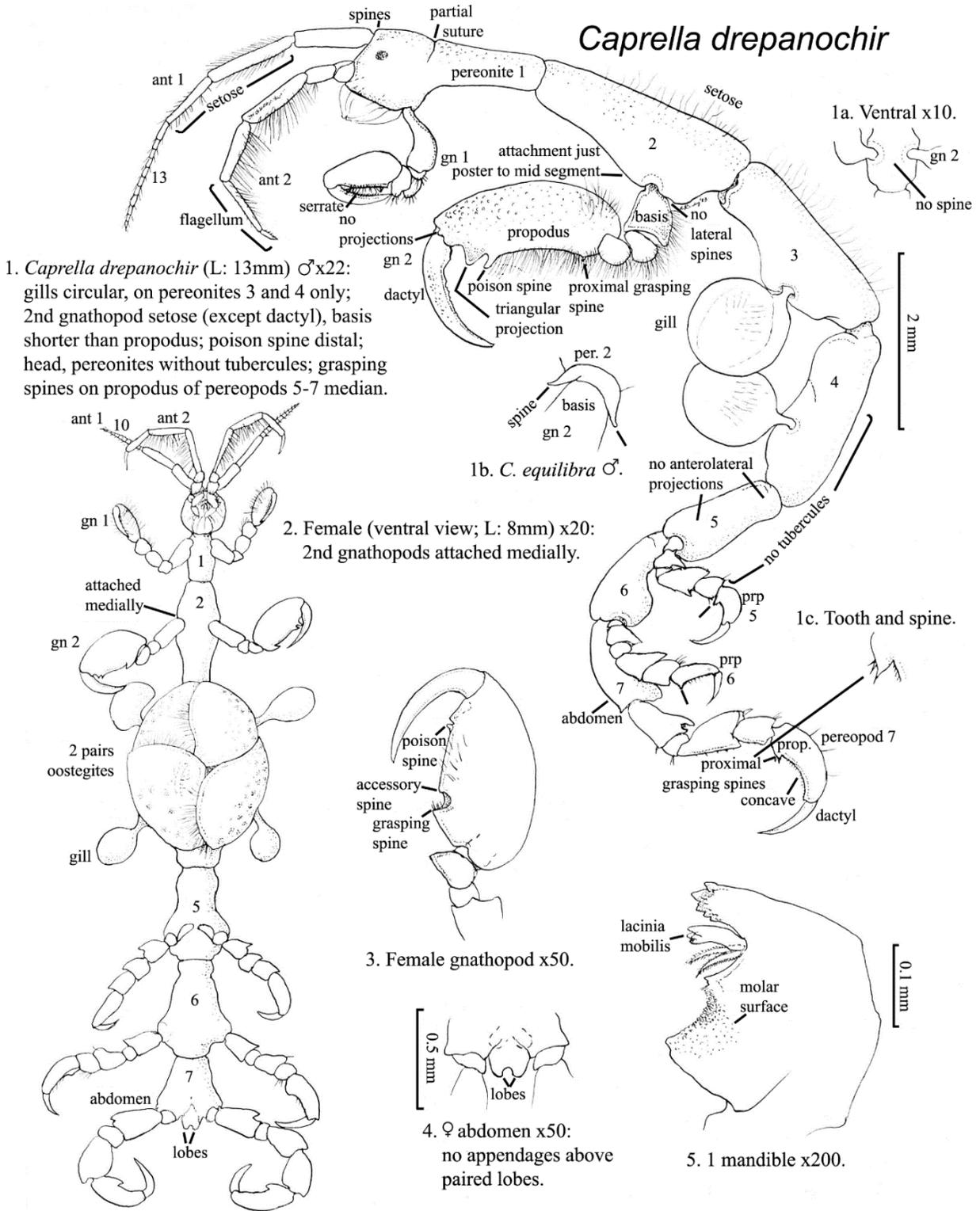
Antenna 1: Less than half total body length (Laubitz 1970). In males, the first antenna is approximately equal to the cephalon combined with pereonite two (Laubitz 1970) (Fig. 1). Articles 2–3 of peduncle are setose while the flagellum is shorter than peduncular articles one and two, and bears 13 articles (Laubitz 1970) (Fig. 1). In the illustrated female, antenna one is a little longer than cephalon and pereonite one and the flagellum has 10 articles (Fig. 2).

Antenna 2: Antenna two in the illustrated specimens is longer than the peduncle of antenna one and has flagellum with short setae (Laubitz 1970) (Figs. 1, 2).

Mouthparts: Mandible with molar (McCain 1975) and without palp (McCain 1975). Left 'lacinia mobilis' with five teeth (Fig. 5) and right 'lacinia mobilis' denticulate but not five-toothed (McCain 1975) (not figured).

Pereon: Pereon with only six segments (not seven as in other amphipods) and no pereopods on pereonites three or four (Caprellidae, McCain 1975; Laubitz 1976). Pereonites cylindrical and longer than deep (Laubitz 1976). Pereonites in this species are without dorsal spines or tubercles, but are covered with fine hairs (Fig. 1). Male pereonite one is not more than twice the length of the head while female pereonite one is shorter than the head (Laubitz 1970) (Fig. 2). Gills on pereonites three and four only. Round in shape and fleshy (*Caprella*, Mayer

Caprella drepanochir



1890; Watling and Carlton 2007) (Figs. 1, 2). Gills in male individuals are more circular and females are broadly rounded (Watling and Carlton 2007). Oostegites (marsupium) present on pereonites 3–4 in females only. The marsupium consists of two pairs of foliaceous plates called oostegites (Caprellidae, Laubitz 1976) that grow from gill bases (Fig. 2) (Arimoto et al. 1976; Watling and Carlton 2007).

Coxae:

Gnathopod 1: Male gnathopod one is small and the propodus and dactyl have serrate grasping margins (Fig. 1) while the female gnathopod is small, setose (Fig. 2).

Gnathopod 2: Male gnathopod two is very large, especially the propodus, width being less than half overall length. The gnathopod is setose, except the dactyl and distal part of propodus (Laubitz 1970). The basis is small, with no lateral spines at the base (Figs. 1, 1b). The propodus is tuberculate anterodistally and palm is with small proximal grasping-spine, large distal poison spine, large triangular projection distal to poison spine and separated by cleft. There are no anterodorsal projections on propodus in this species (Laubitz 1970) (Fig. 1). The dactyl is heavy, slightly curved, with inner margin slightly denticulate and not setose. The gnathopod is attached just posterior to middle of pereonite two (in male) and attached near the middle of pereonite two, but not at its anterior end (in female) (Laubitz 1970) (Fig. 2). The palm of propodus has a proximal grasping spine and an accessory spine, and a minute distal poison spine (Fig. 3). Ventral spines between insertions of second gnathopods are lacking in this species (Fig. 1a). Female gnathopods are much smaller than those of males.

Pereopods 3 through 7: Pereopods 5–7 prehensile (for grasping) and increase in size posteriorly (Fig. 1). Propodus on all pereopods rather stout, with a concave inner edge and a proximal tooth with a pair of grasping spines (Fig. 1c). Female pereopods more slender than those of males (Laubitz 1970) (Fig. 2).

Pleon: The pleon or seventh pereonite is reduced and often unsegmented in caprellids (McCain 1975). Female individuals with one pair of lobes, but no single-articled appendages above these lobes (Figs. 2, 4) (*Caprella*, McCain 1975).

Pleonites:

Urosomites:

Epimera:

Telson:

Sexual Dimorphism: Males much larger and more elongate than females, with a longer first pereonite and an exaggerated second gnathopod. Females when brooding have conspicuous oostegites (see **pereon**) and lack mandible palps (Watling and Carlton 2007).

Possible Misidentifications

In contrast to the more familiar Gammaroidea, the bodies of caprellid amphipods are elongate and cylindrical, their pereonites are very long and their three pairs of pereopods are prehensile. Caprellids have 2–3 pairs of gills on the middle pereonites and lack the abdominal pleopods of gammarid amphipods. Members of three subfamilies (family Caprellidae) occur locally including, Caprellinae, Paracercopinae and Phtisicinae. The caprellid family Cyamidae are parasitic on cetacean mammals. They are very short bodied, dorso-ventrally flattened (like isopods), and have third and fourth pereonites especially adapted for hanging on to their host.

Phtisicinae have three pairs of gills, not two (unlike Caprellinae). In addition, they have no molar surface on the mandible. The Phtisicinae have rudimentary pereopods on pereonites three and four (Laubitz 1970). Of this family, *Perotripus brevis* has been reported from California (McCain 1975; Watling and Carlton 2007). It, as well as *Cercops compactus* (Laubitz, 1970), occurs in Puget Sound. *Caprella compactus* has also been reported from the outer coast of Oregon, at Cape Arago (Laubitz 1970; Martin 1977) and is in the only representative of the subfamily Paracercopinae locally. *Cercops compactus* does not have an elongate body as other caprellids do, its abdomen has five segments, and pereonites five and six are short and stout (Watling and Carlton 2007).

The subfamily Caprellinae is the most speciose with 23 species in the genus *Caprella*, three in *Tritella* and one each in *Deutella* and *Mayerella* (Watling and Carlton 2007).

Tritella pereopods have only one article and their second antennae have swimming setae (Laubitz 1970; McCain 1975). Three

species are found in Oregon: *T. laevis* is strongly stenohaline, and is found offshore from British Columbia, Canada to Monterey Bay, California (Martin 1977). It has anteriorly pointed body spines and short spines on the stout flagellum of its second antennae. This species can display "intersex" features (Laubitz 1970), making males and females difficult to distinguish. *Tritella pilimana* has laterally pointed body spines and its second antennal setae are long on a slender flagellum. It is more euryhaline than *T. laevis* and is found from Alaska to California (Martin 1977). *Tritella tenuissima* is a deep water species, known off shore in southern California. It lacks swimming setae on antenna two and (some believe) should be transferred to the genus *Triliropus* (McCain 1975).

The genus *Metacaprella* was characterized by a pair of appendages above the usual lobes on the female abdomen (McCain 1975) where *Caprella* spp. have only the one pair of lobes (Fig. 4). *Caprella anomala* and *C. kenneryli* were formally members of this genus (*M. anomala* and *M. kenneryli*). Both have a small pair of sharp spines on the heads and are reported from California and from Puget Sound, Washington (Keith 1971; McCain 1975; Martin 1977).

The genus *Caprella* is characterized by the presence of gills on pereonites 3–4, oostegites and mandibles without palps (females) (Watling and Carlton 2007). *Caprella greenleyi* has been reported living on hydroids and algae and on the sea star *Henricia* spp. both in Oregon and in California (McCain 1969, 1975; Martin 1977). Unlike most free-living caprellids, it is quite stout, and has unusual antennae-- both pairs have only a uni-articulate flagellum (McCain 1975).

A few caprellids have a ventral spine between the insertions of the second gnathopods (*C. drepanochir* does not): *C. californica*, *C. equilibra*, *C. mendax*, and *C. pilidigitata* (Laubitz 1970). *Caprella californica* has a long, forward directed cephalic spine (Laubitz 1970). Both the propodus and basis of the male gnathopod two are very long in this species. *Caprella californica* has a wide distribution from the western to eastern Pacific coasts (Martin 1977). *Caprella equilibra* has no cephalic spine (McCain 1975) (like *C. drepanochir*).

But unlike the latter species, it has anterior lateral projections on pereonite five, large lateral spines at the base of the gnathopod two (McCain 1975) (Fig. 1b), and the ventral spines between the gnathopods (Figs. 1, 1a). Northeast Pacific range of *C. equilibra* includes San Juan Islands, Washington and British Columbia, Canada (Martin 1977). *Caprella mendax* has no cephalic spine, no lateral projections on pereonite five, and only small lateral spines at the bases of the second gnathopods. Its dactyl is not setose and its distribution ranges from Vancouver Island, Canada to San Diego, California (Martin 1977). *Caprella pilidigitata* has no lateral spine near the base of gnathopod two and its dactyl is setose.

One group of *Caprella* species has at least a slight cephalic spine (and lacks ventral spines between the second gnathopods, (as above) and includes *C. natalensis*, *C. penantis*, *C. brevisrostris*, *C. pustulata*, *C. simia* and *C. scaura*. *Caprella natalensis* (= *C. angusta* and *C. uniforma*, Watling and Carlton 2007) has a slight cephalic spine and small dorsal pereonite spines, except on pereonite one. Gnathopod two is attached at the anterior end of the second pereonite in males. The northeast Pacific distribution of *C. natalensis* includes British Columbia, Canada to Santa Cruz, California (Martin 1977). *Caprella penantis* is morphologically similar to *C. natalensis* however pereonite five is usually longer than six and seven in the latter species (see Laubitz 1972; Watling and Carlton 2007). *Caprella brevisrostris* has only a very slightly produced rostrum, not a cephalic spine (Arimoto et al. 1976). It differs chiefly from *C. drepanochir* in that it lacks grasping spines on its pereopodal propodi (Fig. 1c). It has been reported from the coasts of Japan (Arimoto et al. 1976), Korea and China (Martin 1977), and from California (McCain 1975), but not from Puget Sound (Keith 1971) or from Oregon (Laubitz 1970). *Caprella pustulata* (Laubitz 1970) has a dorsal, upward directed knob on its head. The head and pereon are covered with large and small tubercles (Keith 1971). The male is setose on the second gnathopods and on much of the body. The antennae have some very long setae. *Caprella pustulata* is reported from British Columbia, Puget Sound and from Oregon (Laubitz 1970), but not from California (McCain 1975; Martin 1977).

Caprella scaura (Templeton, 1836), a cosmopolitan species newly found in North America (Marelli 1981), is very like *C. californica* above, except that it lacks a ventral spine between the gnathopods, and has two pairs of dorsal tubercles on pereonites five (Marelli 1981). Pereonite four in adult males is smooth dorsally in *Caprella simia*, a species introduced to southern California from Japan (Watling and Carlton 2007).

Obvious dorsal tuberculations on the pereonites (lacking in *C. drepanochir*) characterize the group composed of *C. alaskana*, *C. ferrea*, *C. incisa*, *C. mutica*, *C. pilipalma* and *C. verrucosa*. *Caprella alaskana* has quite variable dorsal pereonite spines. It has long first antennae, but the flagellum is shorter than the peduncle, not longer. The male second antenna is shorter than the first two articles of the first antenna. Like *C. drepanochir*, *C. alaskana* has a first pereonite not more than twice the length of its head (Keith 1971). It is an intertidal species, found in Alaska and British Columbia, Canada (Martin 1977). *Caprella ferrea* has a pair of small blunt spines on its head (Laubitz 1970). The dorsal pereonite tubercles become large spines in the posterior pereonites (Keith 1971). The first pereonite in the male is about as long as the head (Keith 1971). *C. ferrea* can be similar to *C. alaskana* above in its juvenile and immature stages, but not as an adult (Laubitz 1970). Found in Alaska, British Columbia and in Puget Sound (Keith 1971; Martin 1977). *Caprella incisa* has small dorsal tubercles on its pereonites, the propodus (on second gnathopod in males) is as long as pereonite two (Keith 1971). Its first antennal peduncle is finely setose (McCain 1975). It has a triangular cephalic projection, directed anteriorly (McCain 1975), which is lacking in *C. drepanochir*. *C. incisa* has been reported from British Columbia, Canada to southern California (Martin 1977). *Caprella mutica*, an Asian species, has now been reported from California (Martin 1977; Marelli 1981), and was found in Coos Bay with *C. drepanochir* (authors). It has also been called *C. acanthogaster humboldtiensis* (Martin 1977). *Caprella mutica* has dorsal projections on pereonites 3–5, but not on the anterior pereonites, which are setose. It has no cephalic projections. The entire second gnathopod (males) is setose in this species (including the dactyl). The pereopodal

grasping spines (on propodus) are medial, not proximal as in *C. drepanochir*. *Caprella pilipalma* has low tubercles dorsally, especially on its posterior segments. It has a small, erect, pointed, dorsally directed cephalic spine (Dougherty and Steinberg 1953) and its second gnathopods are attached posteriorly to the second pereonites in the male, and anteriorly in the female (contrast *C. drepanochir*). The large propodus on the male gnathopod two has no poison spine or grasping spine, but does have many long colorless hairs (Dougherty and Steinberg 1953). *Caprella verrucosa* has large, blunt tubercles on all pereonites, it is the most tuberculate of this group. Unlike many of the genus, *C. verrucosa* and *C. drepanochir* have an antennal peduncle which is scarcely setose (Dougherty and Steinberg 1953). The propodus on the second gnathopod in *C. verrucosa* is shorter than the second pereonite (Keith 1971). This species has an anteriorly directed triangular cephalic projection (Keith 1971). Found in Puget Sound (Keith 1971), California, British Columbia, Japan (Martin 1977). Some specimens of *C. verrucosa* from protected waters have a ventral spine between the second gnathopods, in contradiction to most keys (Marelli 1981).

There are two other *Caprella* species, which, like *C. drepanochir*, have no cephalic spines, no ventral spines between the gnathopods, and no dorsal pereonite projections: *C. gracilior*, and *C. laeviuscula*. *Caprella gracilior* is occasionally found intertidally, but usually inhabits deep water (below 9 m, Laubitz 1970). It has a smooth body, except for two tubercles on pereonite five. The grasping spines on the slender pereopod propodus are medial (not proximal as in *C. drepanochir*). The basis of the male gnathopod two is much longer than the propodus and the dactyl is setose (Laubitz 1970). It has been reported from Alaska, Washington, and California, but not from Oregon (Laubitz 1970). *Caprella laeviuscula* is the most common northeastern Pacific species (Laubitz 1970), and would be expected to be found intertidally in Oregon's estuaries. It is the species most similar to *C. drepanochir* in (according to McCain 1975, which does not include *C. drepanochir*). The main difference is in the gills: they are long and oval in *C. laeviuscula* and round in *C.*

drepanochir. The male second gnathopod in *C. laeviuscula* has an extremely large poison spine (it is larger in *C. drepanochir*). The female gnathopod twp in *C. laeviuscula* is attached near the middle of the pereonite (Laubitz 1970) (contrast Fig. 2). *Caprella laeviuscula* has a wide northern Pacific distribution from Japan, to Alaska, British Columbia and south to Monterey, California (Martin 1977).

Caprella carina, a boreal species, apparently washed ashore in Coos Bay but its local establishment is unknown (Jessen 1969; Watling and Carlton 2007).

Ecological Information

Range: Original description (and presumed type region) from coast of China (Laubitz 1970; Mayer 1890; Guerra-Garcia and Takeuchi 2003). An amphi-Pacific species with a range extending from (Laubitz 1970) Japan, Russia, the Arctic and Alaska as far as Prince William Sound. *Caprella drepanochir* is an introduced species to the northeast Pacific coast and was introduced in ship fouling from Asia (e.g. Japan) to San Francisco Bay, California (Carr et al. 2011) and Oregon (Watling and Carlton 2007).

Local Distribution: Coos Bay sites, including dock-side at the Charleston small boat basin.

Habitat: Substrate determined by food source as caprellids can cling to almost any surface. They can be found on algae, sponges, etc., but do not like sandy or muddy bottoms (McCain 1975).

Salinity: Collected at salinities of 30 (in Coos Bay).

Temperature: Primarily an Arctic species in protected, cold-temperature zones (e.g. Prince William Sound, AK) (Laubitz 1970).

Tidal Level: Intertidal (Laubitz 1970) and subtidal.

Associates: These specimens were collected with *Obelia* sp. from floating docks, but can also occur with the congener *Caprella mutica*. In Japan, they are commonly associated with *Tubularia* sp.

Abundance: Locally common in Coos Bay (Charleston boat basin), especially in July. One of the most abundant epifaunal species in eelgrass (*Zostera marina*) communities in San Francisco Bay, California (Carr et al. 2011) and Willapa Bay, Washington (Ferraro and Cole 2007).

Life-History Information

Reproduction: Development in most amphipods is direct, lacking a larval stage. Little is known about the reproduction and development in *C. drepanochir*. Eggs carried by female in marsupium (Fig. 2), until they hatch at 0.4–0.5 mm.

Larva: No larval stage is observed *per se*, instead small adult-like juveniles hatch from female marsupium and grow to 1 mm long. Some stay in marsupium until mother's first molt (Japan, Kawana, in Arimoto et al. 1976; Wolff 2014).

Juvenile: Some *Caprella* juveniles cling to their mother's body and grow through four molts over a period of 16 days. These juveniles are protected and groomed by their mother (e.g. *Caprella monoceros*, Aoki and Kikuchi 1991) and this extended parental care has been observed in a number of caprellids (Thiel 1997). In other species juveniles do not cling to their mother's body, but remain near her, attached to algae, where they receive protection from predators and other caprellids (e.g. *Caprella decipiens*, Aoki and Kikuchi 1991).

Longevity:

Growth Rate: Amphipod growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens (Ruppert et al. 2004). Caprellids undergo repeated moltings as they grow and individuals of a single species can show great variability in size depending upon their age (Arimoto et al. 1976). Sexually mature females are 7.5 mm in length, while males are 18 mm (Arimoto et al. 1976).

Food: Caprellids can eat many things by different methods. Presence of plumose setae on second antennae provides the ability to filter food and to scrape periphyton from surfaces to which they cling (Caine 1977) (e.g. *Obelia*, in Coos Bay). Some individuals will nip off hydroid polyps as well as diatoms or detritus (Kozloff 1993). When feeding, the caprellid hangs on with prehensile pereopods and uses antennae and gnathopods for eating.

Predators: Caprellids are fed upon by bottom fishes (cod, blennies, skates, sea bass), also by shrimp, anemones (McCain 1975), and hydroids (e.g. *Candelabrum fritchmanii*, Hewitt and Goddard 2001).

Behavior: Movement is inchworm-like: grasping substrate with large anterior gnathopods, then pulling up posterior and grabbing on with pereopods and posterior appendages.

Bibliography

1. AOKI, M., and T. KIKUCHI. 1991. Two types of maternal care for juveniles observed in *Caprella monoceros* (Mayer, 1890) and *Caprella decipiens* (Mayer, 1890) (Amphipoda, Caprellidae). *Hydrobiologia*. 223:229-237.
2. ARIMOTO, I., D. KYOTO, and J. SETO RINKAI. 1976. Taxonomic studies of Caprellids (Crustacea, Amphipoda, Caprellidae) found in the Japanese and adjacent waters. *Nihon Warekararui Shuppanbu, Yokohama*.
3. CAINE, E. A. 1977. Feeding mechanisms and possible resource partitioning of the Caprellidae (Crustacea: Amphipoda) from Puget Sound, USA. *Marine Biology*. 42:331-336.
4. CARR, L. A., K. E. BOYER, and A. J. BROOKS. 2011. Spatial patterns of epifaunal communities in San Francisco Bay eelgrass (*Zostera marina*) beds. *Marine Ecology*. 32:88-103.
5. DOUGHERTY, E. C., and J. E. STEINBERG. 1953. Notes on the skeleton shrimps (Crustacea: Caprellidae) of California. *Proceedings of the Biological Society of Washington*. 66:39-49.
6. FERRARO, S. P., and F. A. COLE. 2007. Benthic macrofauna habitat associations in Willapa Bay, Washington, USA. *Estuarine Coastal and Shelf Science*. 71:491-507.
7. GUERRA-GARCIA, J. M., and I. TAKEUCHI. 2003. The Caprellidea (Malacostraca, Amphipoda) from Mirs Bay, Hong Kong, with the description of a new genus and two new species. *Journal of Crustacean Biology*. 23:154-168.
8. HEWITT, C. L., and J. H. R. GODDARD. 2001. A New species of large and highly contractile hydroid in the genus *Candelabrum* (Hydrozoa : Anthoathecatae) from southern Oregon, USA. *Canadian Journal of Zoology*. 79:2280-2288.
9. JESSEN, M. P. 1969. The ecology and taxonomy of the Caprellidae (order: Amphipoda; Suborder: Caprellidea) of the Coos Bay, Oregon, area. Ph.D. University of Minnesota.
10. KEITH, D. E. 1971. Substrate election in caprellid amphipods of Southern California, with emphasis on *Caprella californica* Stimpson and *Caprella equilibra* Say (Amphipoda). *Pacific Science*. 25:387-394.
11. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
12. LAUBITZ, D. R. 1970. Studies on the Caprellidae, (Crustacean, Amphipoda) of the American North Pacific. National Museum of Natural Sciences (Ottawa) Publications in Biological Oceanography:1-89.
13. —. 1972. The Caprellidae (Crustacea, Amphipoda) of Atlantic and Arctic Canada. National Museum of Natural Sciences (Ottawa) Publications in Biological Oceanography: 1-82.
14. —. 1976. On the taxonomic status of the family Caprogammaridae (Kudrjaschov&Vassilenko) (Amphipoda). *Crustaceana*. 31:145-149.
15. —. 1993. Caprellidea (Crustacea, Amphipoda): towards a new synthesis. *Journal of Natural History*. 27:965-976.
16. MARELLI, D. C. 1981. New records for Caprellidae in California, USA and notes on a morphological variant of *Caprella verrucosa*. *Proceedings of the Biological Society of Washington*. 94:654-662.
17. MARTIN, D. M. 1977. A survey of the family Caprellidae (Crustacea, Amphipoda) from selected sites along the northern California coast. *Bulletin Southern California Academy of Sciences*. 76:146-167.
18. MAYER, P. 1890. Nachtrag zu den Caprelliden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte : Mit 7 Tafeln in

- Lithographie. R. Friedländer u. Sohn, Berlin.
19. MCCAIN, J. C. 1969. A new species of a caprellid (Crustacea, Amphipoda) from Oregon. Proceedings of the Biological Society of Washington. 82:507-509.
 20. —. 1975. Phylum Arthropoda: Crustacea, Amphipoda: Caprellidea, p. 367-376. *In*: Light's manual: intertidal invertebrates of the central California coast. R. I. Smith and J. T. Carlton (eds.). University of California Press, Berkeley California.
 21. MYERS, A. A., and J. K. LOWRY. 2003. A Phylogeny and a new classification of the Corophiidea (Leach, 1814) (Amphipoda). Journal of Crustacean Biology. 23:443-485.
 22. RUPPERT, E.E., R.S. FOX, and R.D BARNES. 2004. Invertebrate zoology: a functional evolutionary approach, 7th Edition. Thomson Brooks/Cole, Belmont, CA.
 23. TAKEUCHI, I. 1993. Is the Caprellidea a monophyletic group. Journal of Natural History. 27:947-964.
 24. THIEL, M. 1997. Another caprellid amphipod with extended parental care: *Aeginina longicornis*. Journal of Crustacean Biology. 17:275-278.
 25. UTINOMI, H. 1943. The fauna of Akkeshi Bay XIII. Caprellidae. Journal of the Faculty of Science, Hokkaido Imperial University. 8:283-300.
 26. WATLING, L., and J. T. CARLTON. 2007. Caprellidae, p. 618-629. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley.
 27. WOLFF, C. 2014. Amphipoda, p. 206-209. *In*: Atlas of crustacean larvae. J.W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.

Updated 2015

Neotrypaea californiensis

The ghost shrimp

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Anomura, Paguroidea
Family: Callinassidae

Taxonomy: *Neotrypaea californiensis* was described as a member of the genus *Callinassa* 1854 by Dana and remained there until an analysis by Manning and Felder (1991) resulted in the three NE Pacific *Callinassa* species moving to the new genus *Neotrypaea*. Tudge et al. (2000) later analyzed 93 characters of adult morphology and found the genus *Neotrypaea* to be non-monophyletic and Sakai (1999) synonymized *Neotrypaea* and *Callinassa*. The monophyly of *Neotrypaea* is still supported by some authors (e.g. Campos et al. 2009) and we follow the most current local intertidal guides, which use *N. californiensis* (Kuris et al. 2007). For complete list of synonymies see Sakai (2005).

Description

Size: Males up to 115 mm and females to 120 mm in length (Barnard et al. 1980; Puls 2001; Wicksten 2011).

Color: Can be white to cream with patches of pinkish red or orange on the abdomen and appendages (see Plate 19, Kozloff 1993; Wicksten 2011). The illustrated specimen (from Coos Bay) is pale pink with light orange abdomen.

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are outstretched and shrimp-like in Callinassidae (Stevens 1928; Kuris et al. 2007).

Cephalothorax:

Eyes: Eyestalks flattened and with acute tips. Pigmented corneas are mid-dorsal within eyestalk (Fig. 2) (Wicksten 2011). Eyes triangular and with diverging tip (Campos et al. 2009).

Antennae: Antennal angles rounded and naked and antennal peduncle shorter

than antennular peduncle (Campos et al. 2009).

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004). The third maxilliped in *N. californiensis* is operculiform, with widened merus extending beyond articulation with carpus and ischium (Manning and Felder 1991; Campos et al. 2009; Wicksten 2011).

Carapace: Smooth and with lateral grooves (Wicksten 2011).

Rostrum: Not prominent, rounded and with small blunt tooth (Wicksten 2011) (Fig. 2).

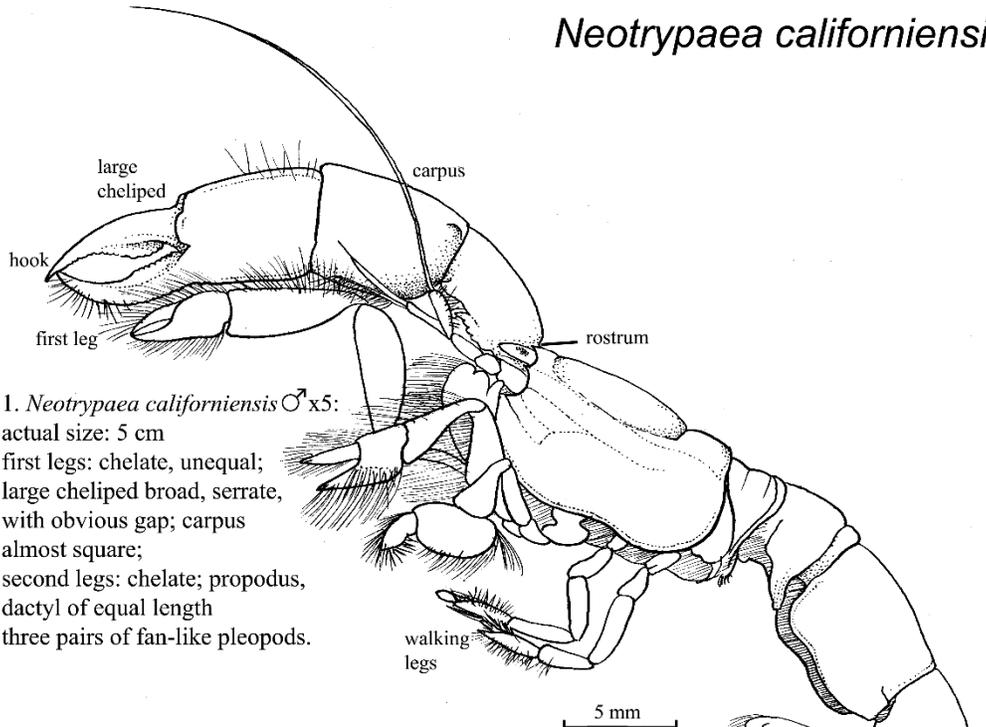
Teeth:

Pereopods: Second pereopod flattened, chelate (Fig. 3) and with row of setae along posterior margin (Campos et al. 2009). Third to fifth pereopods are predominantly used in walking (MacGinitie 1934). Third pereopod with triangular carpus and round, small dactyl. Fourth and fifth pereopods are slender (Wicksten 2011).

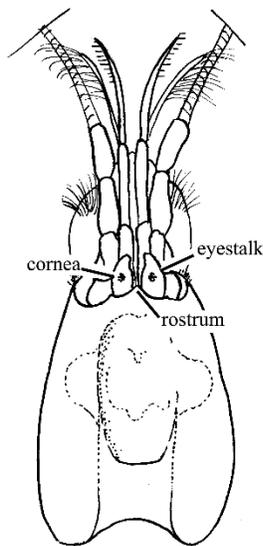
Chelipeds: First chelipeds are chelate and unequal (Fig. 1). The large cheliped is broad, serrate and with an obvious gap in dactyls. The merus has a conspicuous ventral lobe, the carpus is almost square and longer than the palm, and with laterally incurved dorsal margin (Campos et al. 2009). The dactyl has a recurved hook distally (Wicksten 2011) (Fig. 1). Propodi are of nearly equal length (McGinitie 1934). Second chelipeds are both chelate with propodi and dactyls near equal in width (Figs. 1, 3). Female and immature individuals have hand longer than carpus (Wicksten 2011).

Abdomen (Pleon): Abdomen elongate (longer than cephalothorax), not reflexed but extended, symmetrical and externally segmented. It bears three pairs of fan-like pleopods (Fig. 1). First and second pleopods

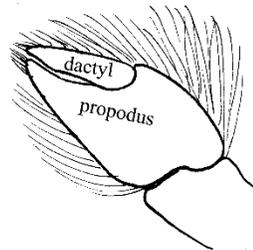
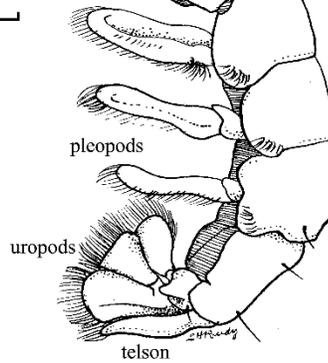
Neotrypaea californiensis



1. *Neotrypaea californiensis* ♂ x5:
 actual size: 5 cm
 first legs: chelate, unequal;
 large cheliped broad, serrate,
 with obvious gap; carpus
 almost square;
 second legs: chelate; propodus,
 dactyl of equal length
 three pairs of fan-like pleopods.



2. Head (dorsal view):
 eyestalks flattened, acute,
 pigmented, divergent;
 corneas dorsal
 rostrum: small, blunt.



3. Second pereopod:
 dactyl (top) closes to
 propodus without a gap;
 dactyl, propodus same
 width.

are vestigial and absent in males. Third to fifth are leaf-like (Fig. 1). In females, the first pleopods are uniramous and the second are biramous (Wicksten 2011).

Telson & Uropods: Telson nearly rectangular, forming a well-developed fan-shape with uropods, which are equal in length to the telson (Fig. 1). Telson composed of two dorsal ribs and posterior marginal tooth. Exopod (outer ramus) also with dorsal ribs.

Sexual Dimorphism: Pleopod (see **Abdomen (Pleon)**) and cheliped (see **Chelipeds**) morphology differs between males and females. Females are also commonly seen with conspicuous bright orange egg masses attached to their pleopods.

Callianassidae-specific character

Burrow: *Neotrypaea californiensis* build and inhabit large, sloppy and permanent burrows with branching side tunnels (Y-shape, Jensen 1995; Puls 2001). Individuals dig tirelessly, turning over acres of northwest oyster beds (Ricketts and Calvin 1971, see **Behavior**). Burrows can be to 0.76–1.00 m deep (MacGinitie 1934; MacGinitie and MacGinitie 1949). They burrow using their first to third legs, aided by mouthparts (MacGinitie 1934; Kozloff 1993) and begin digging backward before turning and removing excess loose sediment from the burrow to the surface (see MacGinitie 1934 for figure).

Possible Misidentifications

Thalassinidea is a former infraorder containing Callianassidae and Upogebiidae and, although shown to be non-monophyletic (Sakai 2004), most mud and ghost shrimps are often referred to collectively as thalassinids.

Upogebiidae is described in Williams (1986) and Campos et al. 2009 and, locally, consists of a single species, *Upogebia pugettensis*, the blue mud shrimp, often co-occurs with *N. californiensis*. *Upogebia pugettensis* is easy to recognize because it is larger and its color (bluish and never red or pink) is strikingly different. Its burrows are also more firm and substantial. The most noticeable morphological difference between the species is the first pair of legs: both of which are small, sub-chelate and equal in *U. pugettensis*. Furthermore, its rostrum is hairy and has a laterally compressed and slender

tip of the short fixed finger of the chela (Wicksten 2011).

Characteristics defining the Callianassidae are described in Sakai 1999 and Campos et al. 2009. There are three species locally, *Neotrypaea californiensis*, *N. gigas* and *N. buffari* (Kuris et al. 2007). *Neotrypaea californiensis* can be distinguished from the other two species by the lack of a prominent rostrum (present in *N. gigas*) and eyestalks that are acute and diverging tips of the eyestalks (rather than short, blunt and not diverging in *N. buffari*) (see Campos et al. 2009). *Neotrypaea gigas* is larger (to 125–150 mm) than the other two, and relatively rare in sandy sublittoral habitats. Its rostrum is sharp, with prominent medial tooth (which *N. californiensis* does not possess), and its first chela closes without a gap. It is more common in its southern distribution, south of Point Conception (Barnard et al. 1980; Kuris et al. 2007; Wicksten 2011). *Neotrypaea gigas* and *N. californiensis* also differ in the morphology of the second pereopod: In *N. californiensis* the propodus and dactyl are of equal length and in *N. gigas*, the propodus is curved and wider than the dactyl (Kuris et al. 2007). Recent examination of these two species using morphological and molecular data suggests that the key characters for differentiating species is the length of eyestalks and shape of the distal outer edges (Pernet et al. 2010).

Ecological Information

Range: Type region is California, with proposed locality San Francisco or Monterey Bay (Wicksten 2011), but type material has been lost. Known range includes Alaska to Tiajuana River, California and Point Abreojos, Baja California, Mexico (Campos et al. 2009)

Local Distribution: Distribution in many Oregon estuaries including Coos Bay, Alsea River (Gaumer et al. 1973b), Nestucca estuary (Gaumer et al. 1973a), Netarts Bay (Gaumer et al. 1974), Umpqua estuary (Umpqua Estuary 1978), Tillamook Bay (Gaumer 1973b) and Yaquina Bay (Gaumer et al. 1974).

Habitat: Mud or sand. Individuals can survive anoxia for nearly six days (Garth and Abbott 1980). In adaptation to living in an environment that is relatively low in oxygen, *N. californiensis* and *U. pugettensis* exhibit low metabolic rates and can both survive

periods of anoxia. *Upogebia pugettensis* has a higher metabolic rate and *N. californiensis* is able to survive longer during periods of anoxia (Thompson and Pritchard 1969a; Zebe 1982).

Salinity: Collected at salinities of 30. An osmotic conformer, lower lethal limit 8.75–10.5 (Thompson and Pritchard 1969b) and the upper limit is 43.75 (Barnard et al. 1980).

Temperature:

Tidal Level: High intertidal. Collected at medium high and upper to mid-intertidal zones (0.0–1.2 m, Ricketts and Calvin 1971).

Associates: The blue mud shrimp, *Upogebia pugettensis*, is found overlapping the range of *N. californiensis*, though it is generally lower intertidally and in muddier sediments.

Common commensals in ghost shrimp burrows include a polynoid worm

Hesperonoe, pinnotherid crabs (*Scleroplax glanulata*), copepods (*Hemicyclops*, *Clausidium*), the shrimp *Betaeus harrimani*, the bopyrid isopod *Ione cornuta*, the goby *Clevelandia*, the echiuroid worm *Urechis caupo*, and the clam *Cryptomya californica* (MacGinitie 1934; Kuris et al. 2007; Campos 2009; Wicksten 2011).

Abundance: Common in Oregon's estuarine mudflats. In Wallapa Bay, Washington, the density of *N. californiensis* (up to 450 shrimp per m²) was always higher than that of the other locally occurring ghost shrimp, *U. pugettensis* (up to 100 shrimp per m²) (Dumbauld et al. 1996).

Life-History Information

Reproduction: Continuously reproductive in central California, especially June and July (MacGinitie 1934; Ricketts and Calvin 1971).

A breeding season in late spring and summer is known to occur in Yaquina Bay, Oregon (Puls 2001). *Neotrypaea californiensis* reach sexual maturity at 2 years and produce 3,900 eggs while *U. pugettensis* produces 7,100 (Dumbauld et al. 1996). Individuals ovigerous from April through August (Willapa Bay, Washington, Dumbauld et al. 1996).

Larva: Larval development in *N. californiensis* proceeds via several zoea (five total) and, a final, megalopa stage, each marked by a molt (Puls 2001). *Neotrypaea californiensis* zoea have rostrum longer than antennules (compare to *Upogebia pugettensis*), abdominal segments with dorsal and/or lateral spines and telson that is broad

and flat with medial tooth at posterior (see paguroid zoeae Fig. 53.2, Harvey et al. 2014: Fig. 11, McCrow 1972; Puls 2001). Larval size (measured from tip of rostrum to tip of telson) proceeds from 2.8–3.6 mm (Zoea I) to 6.8–7.5 mm (Zoea V) (Puls 2001).

Megalopae are shrimp-like in morphology with long pereopods, resembling the adult. First and second pereopods chelate or subchelate (Puls 2001). Larvae are flushed into open ocean by tides, where they spend most of larval period in the plankton and exchange between neighboring bays is common (McCrow 1972; Johnson and Gonor 1982).

Larvae recruit back to the estuary to settle from August to October (Willapa Bay, Washington, Dumbauld et al. 1996) and preferentially settle on mud substrate (rather than shell, Feldman et al. 1997).

Juvenile: Sexual dimorphism and maturation in claw size occurs at 2 years of age, when individuals are 9–10 mm carapace length (Dumbauld et al. 1996).

Longevity:

Growth Rate: Growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens (Ruppert et al. 2004). The growth rate for *N. californiensis* is approximately 2–3 mm (carapace length) per year (Dumbauld et al. 1996).

Food: Detritivore, obtains food by ingesting mud as it burrows the top (richest) layer (MacGinitie 1934; MacGinitie and MacGinitie 1949) and also filter feeds by pumping water through burrow (Powell 1974).

Predators: Adults are used by humans for fish bait and individuals avoid predation by retreating to burrow. Juveniles and larvae are eaten in the plankton (e.g. by fish). Adults are also eaten by bottom feeding fish. Green and white sturgeon collected from Willapa Bay, Washington and the Columbia River estuary had *N. californiensis* within their guts (Dumbauld et al. 2008). Foraging gray whales in British Columbia (Clayoquot Sound) also ingest adult benthic *N. californiensis* (Dunham and Duffus 2001).

Behavior: Ghost shrimp species (e.g. *Neotrypaea*, *Upogebia*) are known to be ecosystem engineers with the ability to regulate and change community (macro and microbial communities) structure by burrowing and deposit feeding (Dumbauld and Wyllie-

Echeverria 2003; Bertics and Ziebis 2009). Their presence and behavior effects biogeochemical composition including sediment grain size, nutrient exchange and organic composition. Bioturbation (Kristensen et al. 2012) turns over and re-suspends sediment, which can increase erosion and sediment instability, having a negative effect on algae and seagrasses that require light for photosynthesis (e.g. *Zostera*, Dumbauld and Wyllie-Echeverria 2003) and suspension feeders (e.g. oysters, Dumbauld et al. 1996; Feldman et al. 2000). All sediment to 76 cm deep is turned over completely in 240 days (MacGinitie 1934). In turn, seagrasses tend to solidify sediment and are not suitable habitats for ghost shrimp species (Berkenbusch et al. 2007). Outside of their burrows, *N. californiensis* specimens are fragile and lay rather helpless on the sediment surface (Kozloff 1993). They can swim for short distances and move quickly backwards by flapping the fan-like posterior (MacGinitie 1934).

Bibliography

1. BARNARD, L. J., D. E. BOWERS, AND E. C. HADERLIE. 1980. *Macrura* and *Anomura*, p. 577-593. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
2. BERKENBUSCH, K., A. A. ROWDEN, AND T. E. MYERS. 2007. Interactions between seagrasses and burrowing ghost shrimps and their influence on infaunal assemblages. *Journal of Experimental Marine Biology and Ecology*. 341:70-84.
3. BERTICS, V. J., AND W. ZIEBIS. 2009. Biodiversity of benthic microbial communities in bioturbated coastal sediments is controlled by geochemical microniches. *Isme Journal*. 3:1269-1285.
4. CAMPOS, E., A. R. DE CAMPOS, AND I. MANRIQUEZ. 2009. Intertidal thalassinidean shrimps (Thalassinidea, Callianassidae and Upogebiidae) of the west coast of Baja, California, Mexico: annotated checklist, key for identification, and symbionts. *Crustaceana*. 82:1249-1263.
5. DUMBAULD, B. R., D. A. ARMSTRONG, AND K. L. FELDMAN. 1996. Life-history characteristics of two sympatric thalassinidean shrimps, *Neotrypaea californiensis* and *Upogebia pugettensis*, with implications for oyster culture. *Journal of Crustacean Biology*. 16:689-708.
6. DUMBAULD, B. R., D. L. HOLDEN, AND O. P. LANGNESS. 2008. Do sturgeon limit burrowing shrimp populations in Pacific Northwest estuaries? *Environmental Biology of Fishes*. 83:283-296.
7. DUMBAULD, B. R., AND S. WYLLIE-ECHEVERRIA. 2003. The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. *Aquatic Botany*. 77:27-42.
8. DUNHAM, J. S., AND D. A. DUFFUS. 2001. Foraging patterns of gray whales in Central Clayoquot Sound, British Columbia, Canada. *Marine Ecology Progress Series*. 223:299-310.
9. FELDMAN, K. L., D. A. ARMSTRONG, B. R. DUMBAULD, T. H. DEWITT, AND D. C. DOTY. 2000. Oysters, crabs, and burrowing shrimp: Review of an environmental conflict over aquatic resources and pesticide use in Washington State's (USA) coastal estuaries. *Estuaries*. 23:141-176.
10. FELDMAN, K. L., D. A. ARMSTRONG, D. B. EGGLESTON, AND B. R. DUMBAULD. 1997. Effects of substrate selection and post-settlement survival on recruitment success of the thalassinidean shrimp *Neotrypaea californiensis* to intertidal shell and mud habitats. *Marine Ecology Progress Series*. 150:121-136.
11. GARTH, J. S., AND D. P. ABBOTT. 1980. *Brachyura: the true crabs*, p. 594-630. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.

12. GAUMER, T. 1974. Yaquina Bay resource use study, p. 26. Oregon State Fish Commission, Portland.
13. GAUMER, T., D. DEMORY, AND L. OSIS. 1973a. 1971 Nestucca River Estuary resource use study. Fish Commission of Oregon, Portland, Oregon.
14. GAUMER, T., D. DEMORY, AND L. OSIS. 1973b. Alsea River Estuary resource use study, 1971. Oregon Fish Commission, Division of Management and Research, Port Orford.
15. GAUMER, T., D. DEMORY, AND L. OSIS. 1974. Netarts Bay Estuary resource use study, 1971. Oregon Fish Commission, Division of Management and Research, Port Orford, Oregon.
16. HARVEY, A. W., C. B. BOYKO, P. MCLAUGHLIN, AND J. W. MARTINS. 2014. Anomura, p. 284-295. *In: Atlas of crustacean larvae*. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
17. JENSEN, G. C. 1995. Pacific coast crabs and shrimps. Sea Challengers, Monterey, CA.
18. JOHNSON, G. E., AND J. J. GONOR. 1982. The tidal exchange of *Callianassa californiensis* larvae between the ocean and the Salmon River Estuary, Oregon. *Estuarine, Coastal and Shelf Sciences*. 14:501-516.
19. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
20. KRISTENSEN, E., G. PENHA-LOPES, M. DELEFOSSE, T. VALDEMARSEN, C. O. QUINTANA, AND G. T. BANTA. 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series*. 446:285-302.
21. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, AND E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
22. MACGINITIE, G. E. 1934. The natural history of *Callianassa californiensis* Dana. *American Midland Naturalist*. 15:166-177.
23. MACGINITIE, G. E., AND N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
24. MANNING, R. B., AND D. L. FELDER. 1991. Revision of the American Callianassidae (Crustacea, Decapoda, Thalassinidea). *Proceedings of the Biological Society of Washington*. 104:764-792.
25. MCCROW, L. T. 1972. The Ghost Shrimp, *Callianassa californiensis* Dana, 1854 in Yaquina Bay, Oregon. Oregon State University, Corvallis, OR.
26. OIMB. 1978. Umpqua Estuary: Unpublished Student Research Project. Oregon Institute of Marine Biology (University of Oregon).
27. PERNET, B., A. DECONINCK, AND L. HANEY. 2010. Molecular and morphological markers for distinguishing the sympatric intertidal ghost shrimp *Neotrypaea californiensis* and *N. gigas* in the eastern Pacific. *Journal of Crustacean Biology*. 30:323-331.
28. POWELL, R. R. 1974. The functional morphology of the fore-guts of the Thalassinid Crustaceans, *Callianassa californiensis* and *Upogebia pugettensis*. University of California Publications in Zoology. 102.
29. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
30. RICKETTS, E. F., AND J. CALVIN. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
31. RUPPERT, E.E., R.S. FOX, and R.D BARNES. 2004. Invertebrate zoology: a functional evolutionary approach, 7th Edition. Thomson Brooks/Cole, Belmont, CA.
32. SAKAI, K. 1999. Synopsis of the Family Callianassidae, with keys to

subfamilies, genera and species, and the description of new taxa (Crustacea: Decapoda: Thalassinidea). Nationaal Natuurhistorisch Museum, Leiden, Netherlands.

Biochemistry and Physiology B-
Biochemistry & Molecular Biology.
72:613-617.

Updated 2015

33. SAKAI, K. 2004. The diphyletic nature of the infraorder Thalassinidea (Decapoda, Pleocyemata) as derived from the morphology of the gastric mill. *Crustaceana*. 77:1117-1129.
34. SAKAI, K. 2005. Callianassoidea of the world (Decapoda, Thalassinidea). *Crustaceana Monographs*. 4:i-vi, 1-285.
35. STEVENS, B. A. 1928. Callianassidae from the west coast of North America. *Publications. Puget Sound Biological Station*. 6:315-369.
36. THOMPSON, J. L., AND A. W. PRITCHARD. 1969. Osmoregulatory capabilities of *Callianassa* and *Upogebia* (Crustacea: Thalassinidea). *Biological Bulletin*. 136:114-129.
37. THOMPSON, R. K., AND A. W. PRITCHARD. 1969. Respiratory adaptation of two burrowing crustaceans *Callianassa californiensis* and *Upogebia pugettensis* (Decapoda, Thalassinidea). *Biological Bulletin*. 136:274-287.
38. TUDGE, C. C., G. C. B. POORE, AND R. LEMAITRE. 2000. Preliminary phylogenetic analysis of generic relationships within the Callianassidae and Ctenochelidae (Decapoda, Thalassinidea, Callianassoidea). *Journal of Crustacean Biology*. 20:129-149.
39. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian zoogeographic provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.
40. WILLIAMS, A. B. 1986. Mud shrimps *Upogebia* from the eastern Pacific: *Thalassinidea upogebiidae*. San Diego Society of Natural History *Memoirs*:1-60.
41. ZEBE, E. 1982. Anaerobic metabolism in *Upogebia pugettensis* and *Callianassa californiensis* (Crustacea, Thalassinidea). *Comparative*

Pagurus hirsutiusculus

Hairy hermit crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Anomura, Paguroidea
Tribe: Paguridea

Taxonomy: The taxonomy in the Paguroidea is complicated, especially among the genera *Eupagurus*, *Bernhardus* and *Pagurus* (described in McLaughlin et al. 2010). The International Commission of Zoological Nomenclature (Opinion 472) placed the generic names *Eupagurus* and *Bernhardus* in the official index of invalid and rejected names, leaving the genera *Pagurus* (Paguridae) and *Dardanus* (Diognidae) as valid (Hemming 1958). Thus, previous synonyms for *Pagurus hirsutiusculus* include *Bernhardus hirsutiusculus* (McLaughlin et al. 2010; Wicksten 2011).

Description

Size: Carapace length 19–32 mm (Barnard et al. 1980; Kozloff 1993). Puget Sound to 50 mm (Ricketts and Calvin 1971) and body often extends past the margin of the shell and cannot be retracted (Kuris et al. 2007).

Color: Body color tan to black or green. Antennae dark green with white stripes. Propodus of walking legs hairy and tipped with white or pale blue and dactyls with vertical red stripes and blue spots at base. Tips of chela tan or orange and walking legs have white band on propodus and sometimes a blue dot. Dactyls whitish and striped with blue and red, antennal flagellum banded with translucent and brown (Wicksten 2011) or greenish with yellow spots (Barnard et al. 1980). Most recognizable patterns are white spots on antennae and white bands around base of second and third legs (see Plate 20 and Fig 117, Kozloff 1993) (Fig. 1).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen is elongated, soft and coiled in Paguridae (Kuris et al. 2007) (Fig. 1).

Cephalothorax:

Eyes: Eyestalks short, stout and with pointed ocular scales (Wicksten 2011).

Antennae: Antennal acicle usually exceeds eyestalk in length. Chemoreceptors on antennule hairs (Barnard et al. 1980).

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004).

Carapace: Shield (hard, anterior portion) wider than long (McLaughlin 1972) (Fig. 1).

Rostrum: Triangular (Fig. 1), acute and not much longer than lateral projections of carapace (Wicksten 2011).

Teeth: Sharp medial frontal tooth (Barnard et al. 1980).

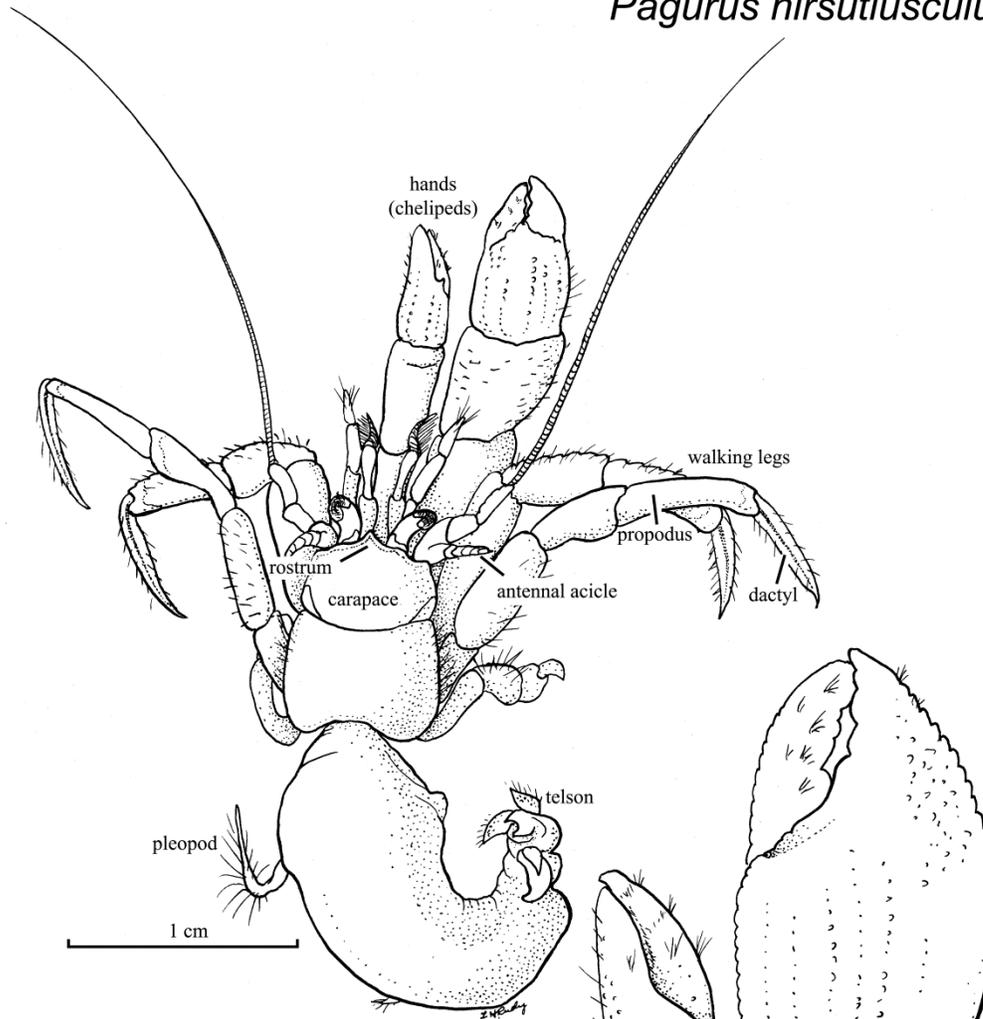
Pereopods: Two pairs of hairy walking legs with dactyls about as long as propodi, which are banded with white. Dactyls slender and about as long as propodi (Wicksten 2011). Two pairs of small posterior legs are adapted for holding shell.

Chelipeds: Left cheliped with small hand and granular surface, slightly hairy and wider than deep (Fig. 2). Right cheliped with large hand, rounded, twice as wide as small hand, granular, slightly hairy and with one large tubercle on ventral surface (Fig. 2). Cheliped stout and shorter than walking legs, is elongated and fingers gaping in male. Merus and carpus with setae, granules, spines and ridges.

Abdomen (Pleon): Abdomen asymmetrical, elongate, twisted, soft and not externally segmented (Fig. 1). Bears small, unpaired pleopods.

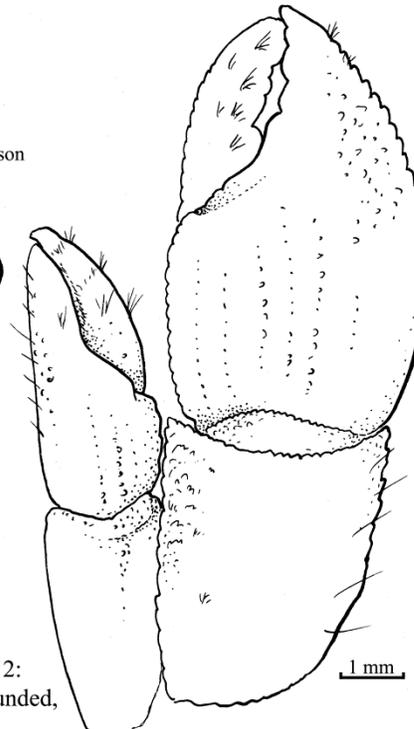
Telson & Uropods: Telson and uropods small. Telson with slightly asymmetrical lobes and a shallow clefts laterally. Posterior margin with notch and spines. Uropods also asymmetrical (Wicksten 2011).

Pagurus hirsutiussculus



1. *Pagurus hirsutiussculus* x4.5:
 light hair all over; color tan, dark green
 antennae white banding; white tips on
 propodi of walking legs, red lines on
 dactyls; eyestalks short, stout; rostrum
 triangular, acute.

2. Left and right chelipeds x12:
 surfaces granular; right rounded,
 twice the width of left.



Sexual Dimorphism: Males usually larger than females (MacGinitie and MacGinitie 1949).

Shell: Usually inhabits *Nassarius fossatus*, *Nucella lamellosa* (e.g. this specimen) (in bays, Schmitt 1921), *Nucella emarginata* or *Littorina* sp. (Kozloff 1993). Individuals often inhabit shells of *Nucella* spp. except in San Francisco Bay, where it uses shells of gastropod species introduced from the Atlantic. Moves to larger shells with increased growth. Innate selection of shell is dependent on size, weight and shell volume (Reese 1962) and even the potential camouflaging properties of the shell (Partridge 1980). Individuals carefully examine and select appropriate shells with their setaceous minor chela. These setae have sensory structures and chemoreceptors that contribute to shell selection (Mesce 1993). Furthermore, shell type (i.e. snail species) may be species-specific and vary throughout ontogeny (Straughan and Gosselin 2014). Thus, available shells may be a limiting resource for hermit crabs (Vance 1972; Worcester and Gaines 1997), but this may only be the case for a specific, preferred, shell type (i.e. species).

Possible Misidentifications

Hermit crabs (superfamilies, Coenobitoidea and Paguroidea) are easily recognizable by their unique morphology and the gastropod shells they inhabit (although they also inhabit tubes, twigs or even bones). They use their last preened pears to grip the shell and their soft abdomen with reduced pleopods and small telson and uropods. Their carapace is usually rather thin, their eyes stalked and have pigmented corneae. They have active antennae, equipped with sensory setae. Their third maxillipeds are leg-like and bear setae and they have chelae that can be large enough to block their external shell aperture or sexually dimorphic.

Three hermit-crab families are currently recognized and occur on the west coast of North America: Diogenidae, Parapaguridae and Paguridae (Wicksten 2011). Parapaguridae species occur on the continental shelf. Diogenidae species, called “left-handed” (left cheliped is equal to or larger than right) hermit crabs, are generally subtidal and often inhabit the shells of moon

snails. The family Diogenidae includes three local species, *Isocheles pilosus*, *Paguristes ulreyi*, and *P. bakeri*). The Paguridae, or “right-handed” (right cheliped is larger than left) hermit crabs, on the other hand, are a speciose family locally, with 10 species, inhabiting the intertidal zone to the continental shelf. Nine of the 10 local pagurid species belong to the genus *Pagurus* (Kuris et al. 2007). The hermit crabs of the genus *Pagurus* are hard to tell apart. However, many local species can be easily differentiated by their bright red or orange antennae and, likewise, many are similar to *P. hirsutiuseulus* in their lack of red antennae.

Pagurus hirsutiuseulus can be distinguished from other *Pagurus* species in that the carapace shield is conspicuously wider than long and has antennae that are banded green and white. Furthermore, individuals are often not able to fully retract into their shells. They are found inhabiting the shells of *Nucella* spp. and may have *Crepidula* spp. living on the inside or outside of their shell. This species co-occurs with *P. samuelis*, but is the more common species in protected areas and bays.

Pagurus beringanus is also a low intertidal species, found at depths up to 364 m. This species has translucent antennae with a conspicuous lateral red mark and usually inhabits shells of *Nucella lamellosa*, *Ceratostoma foliata* and *Fusitriton oregonensis*. It is found on rocky substrates as well as sublittorally and has a whitish body, red banded walking legs, and has inverted V-shaped tubercles on its hands (Wicksten 2011; Kuris et al. 2007).

Pagurus quaylei is a subtidal species (to 97 m) with antennae irregularly banded and dark brown, reddish brown eyestalks and corneae with two bands. A common species amongst sand and polychaete tubes.

Pagurus samuelis, *P. hemphilli*, *P. granosimanus*, *P. armatus*, and *P. caurinus* all have red or orange antennae, where *P. hirsutiuseulus* does not. *P. samuelis* is a high intertidal species that is common and abundant on the open coast, with red antennae and carapace with white stripes. It inhabits shells of *Tegula* spp and may have *Crepidula* spp. living on top of or inside the shell (Wicksten 2011). This species co-occurs with *P. hirsutiuseulus* and is dominant to them in terms of shell competition and

exchange (Kuris et al. 2007). *Pagurus hemphilli* is a low intertidal and mostly subtidal species (to 50 m) with red flagellum of antennae and corneae with distinct yellow rings. This species usually inhabits the shells of *Tegula* and *Astraea* spp, which are often themselves covered with red algae or small mollusks (e.g. *Crepidula adunca*, *Acmaea mitra*). *Pagurus granosimanus* is one of the most common local hermit crab species in the mid-littoral zone and within tide pools. This species has bright red antennae and commonly inhabits the shells of *Tegula* spp. *Pagurus armatus* is a low intertidal species, found at depths up to 146 m, and usually inhabits the shells of *Polinices* spp., and are often covered with the pink hydroid *Hydractinia* sp. *Pagurus caurinus* is a subtidal species, to 126 m, and while it has a northern distribution it is rare at that extent of its range. *Pagurus ochetensis* is a low intertidal and subtidal species which often inhabits moon snail shells (Kuris et al. 2007). Their chelipeds have a red stripe, and their corneae are yellowish green.

Ecological Information

Range: Type locality is Puget Sound, Washington. Known range includes the Pribilof Islands and Bering Strait to northern Japan (Barnard et al. 1980). Pacific Northwest to Monterey, California (McLaughlin 1972). Northern and southern populations used to be split into two subspecies: *P. hirsutiusculus hirsutiusculus* (northern) and *P. hirsutiusculus venturensis* (Monterey Bay, California southward) (Barnard et al. 1980). These subspecies were split into two formal species and, currently, *P. hirsutiusculus* is replaced in its southern distribution by *P. venturensis* (Wicksten 2011).

Local Distribution: Coos Bay sites include South Slough, near the channel at Collver Point and the mudflat of Metcalf Preserve.

Habitat: Protected areas with silt or in bays or harbors (Kozloff 1993; Wicksten 2011). Tidepools, under rocks (with coarse gravel), under seaweed (Kozloff 1993). South Slough specimens occur within *Zostera* bed in mudflats. Individuals appear to prefer algal cover (Orians and King 1964) and sandy tidepools (Reese 1962). Also present on the rocky coast, in tide pools, bays and with coarse sand and gravel (Kuris et al. 2007).

Salinity: Collected at 30, but tolerates brackish conditions (Barnard et al. 1980)

Temperature:

Tidal Level: Upper and middle intertidal zone to 110 m (McLaughlin 1972; Kuris et al. 2007; Wicksten 2011). In South Slough at +0.15 m and -4.5 m.

Associates: In eelgrass, associates include *Littorina* spp. and amphipods (South Slough). Associates includes those found within the shell and living with the hermit crab (e.g. polynoid worms, *Halosydna* spp.) or sessile organisms found on top of or within the shell (e.g. barnacles, limpets and slipper shells, *Crepidula* spp.) (Wicksten 2011). Polydorid worms can infect hermit crabs heavily (*Polydora commensalis*). The parasitic isopod, *Pseudione giardi*, is found with Puget Sound specimens (Barnard et al. 1980). Other parasites and their associates include the rhizocephalan parasite, *Peltogaster puguri* (22% females infected, 11.6% males, Alaska) as well as *Peltogasterella gracilis* and the hyperparasite bopyrid isopod, *Liriopsis pygmaea* in southeastern Alaska (see Fig. 1, Warrenchuk and Shirley 2000).

Abundance: Usually abundant in tidepools (Kozloff 1993) and is one of the common hermit crabs (MacGinitie and MacGinitie 1949; Kuris et al. 2007).

Life-History Information

Reproduction: Male deposits sperm near the female abdomen after molting. The sperm is stored and the female fertilizes eggs once they are laid. Females are ovigerous from December through April (California, Barnard et al. 1980). Brooding begins in late fall and larvae hatch in February, with most females carrying several (~ five) broods a year through spring and summer months. Each brood contains up to 660 eggs and is dependent on female size (Fitch and Lindgren 1979).

Larva: Larval development in *P. hirsutiuseulus* has been described (Lough 1975; Fitch and Lindgren 1979) and proceeds via four zoea and, a final, megalopa stage, each marked by a molt (Puls 2001). *Pagurus hirsutiuseulus* zoea are shrimp-like (see paguroid zoeae Fig. 53.2–3, Harvey et al. 2014: Fig. 1, Fitch and Lindgren; Puls 2001), with telson posterior having seven 7 + 7 spines, with the fifth spine longest and secondary setae on the inner uropod margin.

Zoeal size at each stage proceeds as follows (13°C, Fitch and Lindgren 1979; McLaughlin et al. 1988): 1.9–2.4 mm (Zoea I), 2.6–2.9 mm (Zoea II), 3.2–3.8 mm (Zoea III) and 4.1–5.2 mm (Zoea IV). The zoea of the Paguridae are morphologically similar and easiest to identify by the color and distribution of their chromatophores (visible only in live specimens) (see Fig. 21, Puls 2001). The megalopae have small and reduced telson and uropods (as in adults), and chelipeds that are smooth, with no teeth or hairs (see Fig. 53.7 Harvey et al. 2014). Megalopae are 1.32 mm in length and 1.0 mm in width and are often infested with bopyrid isopod *Pseudione giardi* (Nyblade 1987; Puls 2001). Among competent larvae, settlement can be delayed due to lack of shells or unavailability of food (Harvey and Colasurdo 1993; Worcester and Gaines 1997).

Juvenile: Antennae dark green with white stripes and walking legs white-striped, but never blue. Merus of both chelipeds is dark brown, other leg segments are light brown (Bollay 1964).

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: A detritivore, eats detritus and scavenges for dead plant and animal material (Kozloff 1993). Some estuarine types filter plankton with their mouthparts (MacGinitie and MacGinitie 1949).

Predators: Other crabs.

Behavior: Lively and active, especially shallow water varieties (deepwater animals are more sluggish, MacGinitie and MacGinitie 1949) and will abandon shell in quiet waters (Ricketts and Calvin 1971). Based on a study with Alaskan and southern Californian *P. hirsutiusculus*, it was suggested that evolutionary shell loss may result from large, active species with northern populations (Blackstone 1989).

Bibliography:

1. BARNARD, L. J., D. E. BOWERS, AND E. C. HADERLIE. 1980. Macrura and Anomura, p. 577-593. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
2. BLACKSTONE, N. W. 1989. Size, shell-living and carcinization in geographic populations of a hermit crab, *Pagurus hirsutiusculus*. *Journal of Zoology*. 217:477-490.
3. BOLLAY, M. 1964. Distribution and use of gastropod shells by the hermit crabs *Pagurus samuelis*, *Pagurus granosimanus*, and *Pagurus hirsutiusculus* at Pacific Grove California. *Veliger*, supplement 6:71-76.
4. FITCH, B. M., AND E. W. LINDGREN. 1979. Larval development of *Pagurus hirsutiusculus* (Dana) reared in the laboratory. *Biological Bulletin*. 156:76-92.
5. HARVEY, A. W., C. B. BOYKO, P. MCLAUGHLIN, AND J. W. MARTINS. 2014. Anomura, p. 284-295. *In: Atlas of crustacean larvae*. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
6. HARVEY, A. W., AND E. A. COLASURDO. 1993. Effects of shell and food availability on metamorphosis in the hermit crabs *Pagurus hirsutiusculus* (Dana) and *Pagurus granosimanus* (Stimpson). *Journal of Experimental Marine Biology and Ecology*. 165:237-249.
7. HEMMING, F. 1958. Official index of rejected and invalid family-group names in zoology. First installment: names 1-273. International Trust for Zoological Nomenclature, London.
8. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to Northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
9. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, AND E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal*

- invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
10. LOUGH, R. G. 1975. Dynamics of crab larvae (Anomura: Brachyura) off the central Oregon coast, 1969-1971. Ph.D. Oregon State University, Corvallis, OR.
 11. MACGINITIE, G. E., AND N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 12. MCLAUGHLIN, P. A. 1972. The Hermit Crabs of the genus *Pagurus* (Crustacea, Decapoda, Paguridae) from northwestern North America, with a partial revision of the genus. Ph.D. George Washington University.
 13. MCLAUGHLIN, P. A., R. H. GORE, AND J. A. CRAIN. 1988. Studies on the provenzanoi and other pagurid groups: II. A reexamination of the larval stages of *Pagurus hirsutiusculus hirsutiusculus* (Dana) (Decapoda, Anomura, Paguridae) reared in the laboratory. *Journal of Crustacean Biology*. 8:430-450.
 14. MCLAUGHLIN, P. A., T. KOMAI, R. LEMAITRE, AND D. L. RAHAYU. 2010. Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea) Part I: Lithododeia, Lomisoidea and Paguroidea. *Raffles Bulletin of Zoology*: 5-107.
 15. MESCE, K. A. 1993. Morphological and physiological identification of chelar sensory structures in the hermit crab *Pagurus hirsutiusculus* (Decapoda). *Journal of Crustacean Biology*. 13:95-110.
 16. NYBLADE, C. F. 1987. Phylum or Subphylum Crustacea, Class Malacostraca, Order Decapoda, Anomura, p. 441-450. *In: Reproduction and Development of Marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 17. ORIAN, G. H., AND C. E. KING. 1964. Shell selection and invasion rates of some Pacific hermit crabs. *Pacific Science*. 18:297-306.
 18. PARTRIDGE, B. L. 1980. Background camouflage: an additional parameter in hermit crab shell selection and subsequent behavior. *Bulletin of Marine Science*. 30:914-916.
 19. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 20. REESE, E. S. 1962. Shell selection behavior of hermit crabs. *Animal Behavior*. 10:347-360.
 21. RICKETTS, E. F., AND J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 22. RUPPERT, E. E., R. S. FOX, AND R. D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*. Thomson Brooks/Cole, Belmont, CA.
 23. SCHMITT, W. L. 1921. The marine decapod crustacea of California. *University of California Publications in Zoology*. 23:1-470.
 24. STRAUGHAN, N. A., AND L. A. GOSSELIN. 2014. Ontogenetic changes in shell preferences and resource partitioning by the hermit crabs *Pagurus hirsutiusculus* and *P. granosimanus*. *Journal of Experimental Marine Biology and Ecology*. 451:1-8.
 25. VANCE, R. R. 1972. Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. *Ecology*. 53:1062-1074.
 26. WARRENCHUK, J. J., AND T. C. SHIRLEY. 2000. Parasitism by the rhizocephalan *Peltogaster paguri* (Rathke, 1842) and hyperparasitism by the bopyrid isopod *Liriopsis pygmaea* (Rathke, 1843) on *Pagurus hirsutiusculus* (Dana, 1851) in southeastern Alaska. *Crustaceana*. 73:971-977.
 27. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of

Oceanography, UC San Diego, San Diego, CA.

28. WORCESTER, S. E., AND S. D. GAINES. 1997. Quantifying hermit crab recruitment rates and megalopal shell selection on wave-swept shores. *Marine Ecology Progress Series*. 157:307-310.

Updated 2015

Petrolisthes cinctipes

The flat porcelain crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Anomura, Hippoidea
Family: Porcellanidae

Taxonomy: *Petrolisthes cinctipes* is and has been a widely used name for this species. There are, however, several junior synonyms including *Porcellana cinctipes*, *Porcellana rupicola*, and *Petrolisthes rupicolus* (for all synonyms see Haig 1960; Wicksten 2011).

Description

Size: Individuals up to 24 mm in length (carapace width) (Puls 2001; Wicksten 2011). The illustrated specimen (from Coos Bay) is 14 mm in length and weighs 1.7 g.

Color: Dark blue-brown and somewhat iridescent (see Plate 20, Kozloff 1993). Antennae dark red, maxillipeds bright red-orange and legs blue banded with white (Schmitt 1921). White comma-like marks are sometimes present ventrally and chelipeds bear a red spot at dactyl base, while walking legs have a yellow median band on propodus. Dactyls yellow with narrow brown band. Individuals near molting are blue in color (Wicksten 2011).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The body of the Porcellanidae is crab-like and convex longitudinally with small fifth legs resting on carapace (Fig. 1) and the abdomen and associated appendages are reduced and folded ventrally. The body and chelae of *Petrolisthes* are flattened (Kuris et al. 2007).

Cephalothorax:

Eyes: The eyestalks of *P. cinctipes* contain neurosecretory cell bodies (z-organs) that regulate regeneration, molting and oocyte maturation (Kurup 1964a).

Antennae: Very long, and often folded posteriorly over carapace sides (Fig. 1). First (basal) joint of antennal peduncle is short and not reaching upper margin of carapace.

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004). Second maxillipeds in *P. cinctipes* are highly developed for filter feeding (see **Food**) with long fine hairs and specialized shape for channeling water currents (Fig. 4). The color of the palps of maxilliped three are of taxonomic importance: blue in *P. eriomerus* and orange in *P. cinctipes* (Kozloff 1993; Kuris et al. 2007).

Carapace: Round with carapace front triangulate (*Petrolisthes*, Haig 1960). Carapace surface is finely granulate and not rough. No epibranchial (anterolateral) spines and epimera and lateral portions of carapace are entire (Figs. 1, 2). Carapace about as long as wide (Wicksten 2011).

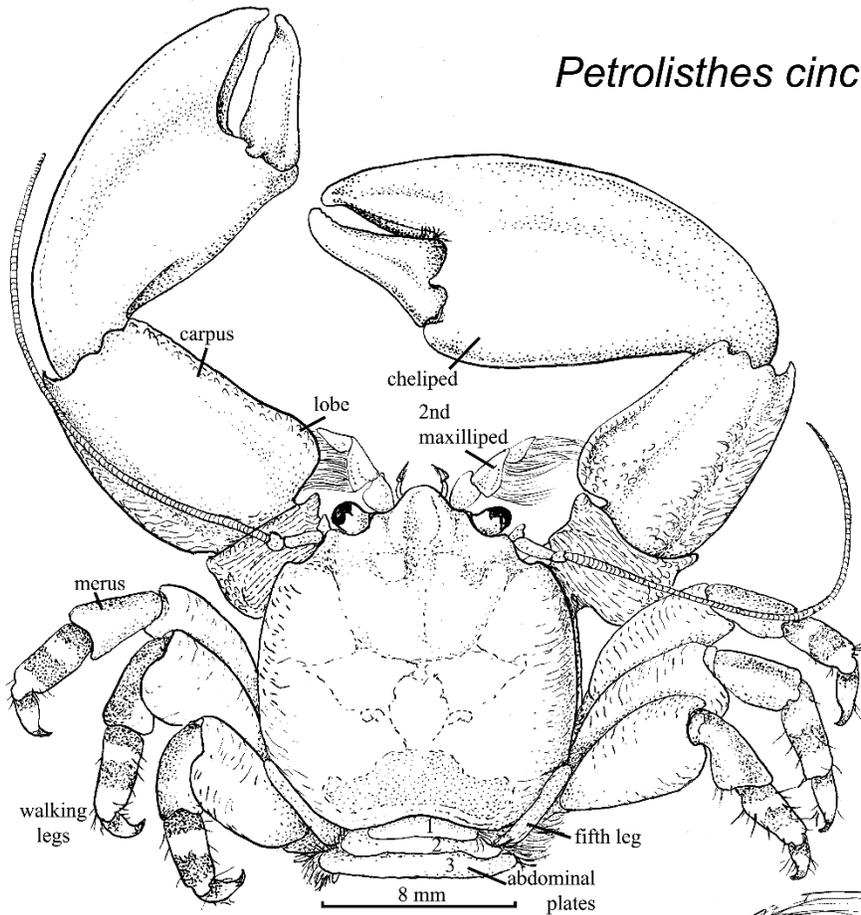
Frontal Area: Triangular and strongly deflexed with conspicuous median groove (Fig. 1).

Teeth:

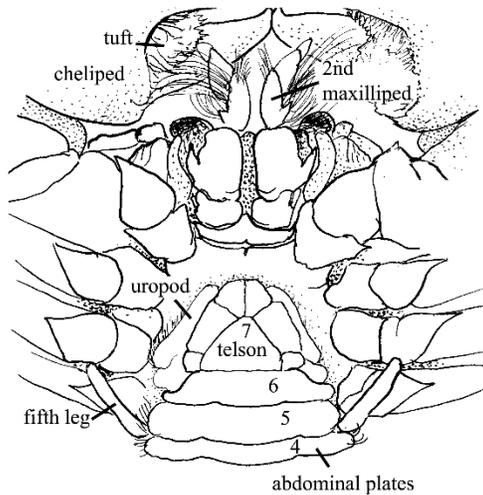
Pereopods: Walking legs 2–4 with a few coarse spines on dactyl, propodus and carpus, but not on merus (Fig. 1). Merus of third leg is inflated and carpus is without setae while propodus and dactyl bear setae. Fifth legs small, elevated and rest on carapace (Figs. 1, 3).

Chelipeds: Equal (or almost), broad and flattened, not thick and rough (*Petrolisthes*, Schmitt 1921; Kuris et al. 2007), covered with fine granules (as in carapace) but without setae. Carpus almost invariably 1 1/2 times longer than wide and anterior and posterior margins converge distally (Schmitt 1921; Kuris et al. 2007) (Fig. 1). Posterior margin with ridge of tubercles flanked by teeth distally. Prominent lobe at inner angle (*P. cinctipes*, Kuris et al. 2007) (Fig. 1). A short tuft of hair between fingers present ventrally, but chelae are generally hairless (Figs. 1, 2). Merus with conspicuous lobe on anterior margin. (Wicksten 2011).

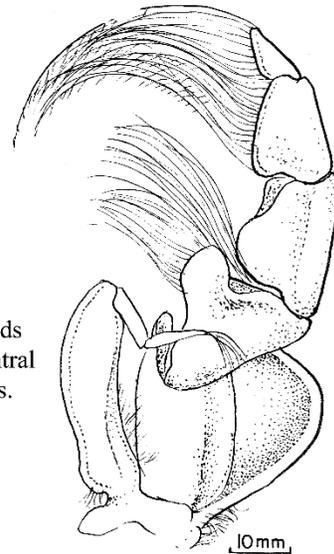
Petrolisthes cinctipes



1. *Petrolisthes cinctipes* x4.5:
actual carapace width 14 mm; body flat, smooth, crab-like;
carapace round, abdomen folded under; color blue-brown,
iridescent, 2nd maxillipeds red-orange; walking legs
striped, merus naked; fifth legs small, elevated.



2. Ventral view x4.5:
folded abdominal plates
(4-7 shown); telson, uropods
visible; chelipeds with ventral
tuft of hair between fingers.



3. Second maxilliped x12:
highly developed articles;
long, fine hairs; bright red-orange.

Abdomen (Pleon): Abdomen symmetrical, short and permanently folded under thorax. Seven abdominal plates (*Petrolisthes*) (Figs. 1, 2).

Telson & Uropods: Seventh plate of telson forms tail fan (Fig. 2). Uropods attached to abdominal segment five.

Sexual Dimorphism: Not obvious superficially. Inside telson, males have single pleopods on abdominal plate two and females have long, branched pleopods on plates 3–5 (not shown).

Possible Misidentifications

Porcelain crabs (Porcellanidae) are flattened dorso-ventrally and are often found in small cracks and crevices. Their third maxillipeds bear long setae, which they use to filter feed and their fifth walking legs are modified into brushes for grooming. There are two genera of porcelain crabs in our area, *Petrolisthes* and *Pachycheles*. Members of the *Pachycheles* have a thick, rough body and chelae, chelae are unequal, tuberculate or granular and hairy, not smooth. Furthermore, the carpus of the chela is as long as broad, not longer than broad as in *Petrolisthes*.

There are three local species: *P. holosericus*, *P. pubescens* and *P. rudis* (Kuris et al. 2007).

Petrolisthes species, on the other hand, have a flattened body and chelae, chelae of equal size with carpus longer than it is wide. *Petrolisthes cinctipes* is recognizable by characteristics of the cheliped carpus. The carpus has a long anterior lobe that extends more than 1/4 total carpus length, is smooth and hairless and with margins that converge distally (Kuris et al. 2007). Five *Petrolisthes* species are reported to occur from central California to Oregon including *P. cinctipes*, *P. cabrilloi*, *P. eriomerus*, *P. manimaculis* and *P. rathbunae*.

Of those, *P. eriomerus* is superficially quite like *P. cinctipes* (Kozloff 1993). This crab lives under rocks in gravelly substrates and is a little smaller than *P. cinctipes*. The carpus of the chelipeds in *P. eriomerus* is twice as long as wide (not 1 1/2 times as long) and the carpus margins are parallel, not converging. Also, there is no prominent lobe at the inner angle and the carpus has scattered tubercles, not a finely granulated surface as in *P. cinctipes*. Ventrally, the outer edge of the maxillipeds in *P. eriomerus* is bright blue, not red orange (Kozloff 1993;

Kuris et al. 2007). These two species exhibit a non-overlapping vertical distribution, where *P. eriomerus* occurs in the low intertidal and *P. cinctipes* is found in the mid to high intertidal (Jensen and Armstrong 1991).

P. cabrilloi, *P. manimaculis* and *P. rathbunae* are all reported from California: *Petrolisthes cabrilloi* from Morro Bay, California south to Baja California, Mexico and apparently replaces populations of *P. cinctipes* south of Point Conception, California; *P. manimaculis* from Bodega Bay, California south to Baja California, Mexico; *P. rathbunae* from Monterey, California to Isla Guadalupe, Mexico (Wicksten 2011).

Ecological Information

Range: Type locality is erroneously indicated as in Hawaii, but is likely to be near Monterey, California (Wicksten 2011). Known range includes British Columbia to Point Conception, California and also islands offshore of southern California, and Baja California (Haig 1960).

Local Distribution: Outer, more marine portions of large estuaries. Occurs locally in Coos Bay (e.g. Pigeon Point) and in Netarts Bay.

Habitat: Protected, semi-protected rocky coasts under rocks and amongst mussel beds (Ricketts and Calvin 1971; Kuris et al. 2007). Prefers open shores and clear water (Haig 1960) and is not tolerant of sand and silt (Jensen and Armstrong 1991; Wicksten 2011).

Salinity: Collected at salinities of 30.

Temperature: A mid to high intertidal species, *P. cinctipes* is exposed to a wide range of temperature (0–32°C, Stillman and Somero 2000). Recent research involving physical factors associated with climate change has used *P. cinctipes* as a model organism (e.g. Somero 2010). Stress by thermal variation, more than other physical factors (e.g. pH, salinity), negatively effects *P. cinctipes* (Paganini et al. 2014). However, when acclimated for a short period of time (6 hrs), *P. cinctipes* can increase thermotolerance (Ronges et al. 2012). Research involving elevated pCO₂, salinity and lower pH, all of which simulate predicted physical changes associated with climate change, have focused on *P. cinctipes* life-history stages (e.g. Miller et al. 2014). Long exposure (40 d) to low pH reduced juvenile

survival and heart rate. Furthermore, embryonic volumes do not increase at a normal developmental rate when exposed to lower pH (Ceballos-Osuna et al. 2013).

Tidal Level: Mid and upper tidal levels and almost exclusively littoral (Haig 1960). Found only at shore stations and not by dredging (San Francisco Bay, Schmitt 1921).

Associates: Associates include mussels, tunicates, sponges, nudibranch *Onchidoris*, chiton *Mopalia*, shore crabs *Hemigrapsus*, *Cancer oregonensis*, predatory gastropod *Nucella*, and the sea star *Pisaster ochraceus*.

Abundance: Very common (Haig 1960) (up to 860 individuals per m², Monterey, California) (Barnard et al. 1980). When found, *P. cinctipes* is usually abundant (MacGinitie and MacGinitie 1949; Kuris et al. 2007).

Life-History Information

Reproduction: Females ovigerous every month of the year but April, May, September, October and November (Haig 1960; Barnard et al. 1980) and evidence shows that multiple males (1–3) may contribute to each brood (Toonen 2004). In Coos Bay, March is the month in which the greatest number of females are found with developing young. Eggs are a little over 800 µm in diameter, deep scarlet to maroon when extruded and become brownish red as they advance developmentally (Gonor and Gonor 1973a; Barnard et al. 1980).

Larva: *Petrolisthes cinctipes* larvae were described by Gonor and Gonor (1973a, b). Development proceeds via two zoeal larval stages and a filter feeding megalopa, each marked by a molt (Puls 2001). Porcelain crab zoea are recognizable as larval stages by their elongate anterior and posterior carapace spines (see Fig. 53.1-3, Harvey et al. 2014; Puls 2011; Wicksten 2011) and have been described as "preposterous unicorns" (Ricketts and Calvin 1971) with a long spine to discourage predators. Other characters of zoeal morphology include a telson posterior margin that is rounded and with long plumose setae. *Pachycheles* and *Petrolisthes* species can be distinguished by the presence of terminal brushes on telson setae, in that *Pachycheles* species have only two and *Petrolisthes* species have brushes on all setae (Puls 2001). The megalopa of *Petrolisthes* species have long, slender

chelipeds that are dorso-ventrally flattened (as in adults) and *P. cinctipes* megalopae have a cheliped carpus with a single spine on the inner margin and an inconspicuous central notch in posterior margin of the telson (Puls 2001). Recently molted megalopae are thigmotactic, settlement is gregarious and individuals remain in high-density aggregations into adulthood (Jensen 1989, 1991; Donahue 2004). Larval settlement was not effected by upwelling conditions, and instead larval abundance increased prior to spring tides, suggesting tidal transport shoreward for settlement (Mace and Morgan 2006). *Petrolisthes cinctipes* larvae do not vertically migrate and maintain their position in nearshore habitats by remaining at depth, where water flow would not push them offshore (Shanks 2009; Miller and Morgan 2013).

Juvenile: Following settlement, megalopae lose the ability to swim as their pleopods degenerate and their body color changes (Fig. 6, Jensen 1991).

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autonomized (Kuris et al. 2007). Porcellanid crabs readily autotomize their chelipeds, to avoid predation, and *Petrolisthes cinctipes* is no exception (Kuris et al. 2007) and autotomy tends to be more common among female and small individuals (Wasson and Lyon 2005). For complete molt staging scheme in *P. cinctipes*, see Kurup 1964b.

Food: A filter feeder that sifts plankton and detritus from water with fan-like second maxillipeds. Feeding behavior evoked by presence of amino acids, sugars (Hartman and Hartman 1976). Despite their mobility, *Petrolisthes cinctipes* is a gregarious species, and increases in conspecific density have been shown to reduce growth rate and feeding frequency (Donahue 2004).

Predators:

Behavior:

Bibliography:

1. BARNARD, L. J., D. E. BOWERS, AND E. C. HADERLIE. 1980. *Macrura* and *Anomura*, p. 577-593. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
2. CEBALLOS-OSUNA, L., H. A. CARTER, N. A. MILLER, AND J. H. STILLMAN. 2013. Effects of ocean acidification on early life-history stages of the intertidal porcelain crab *Petrolisthes cinctipes*. *Journal of Experimental Biology*. 216:1405-1411.
3. DONAHUE, M. J. 2004. Size-dependent competition in a gregarious porcelain crab *Petrolisthes cinctipes* (*Anomura*, *Porcellanidae*). *Marine Ecology Progress Series*. 267:219-231.
4. GONOR, J. J., AND S. L. GONOR. 1973a. Variations in appendage setal counts in zoea larvae of four porcellanid crabs (*Decapoda*, *Anomura*) from Oregon, USA. *Crustaceana* (Leiden). 25:245-252.
5. GONOR, S. L., AND J. J. GONOR. 1973b. Descriptions of larvae of four north Pacific *Porcellanidae* (*Crustacea*, *Anomura*). *Fishery Bulletin*. 71:189-223.
6. HAIG, J. 1960. The *Porcellanidae* (*Crustacea*, *Anomura*) of the Eastern Pacific. *Allan Hancock Pacific Expedition*. 24:1-440.
7. HARTMAN, B., AND M. S. HARTMAN. 1976. The stimulation of filter feeding in the porcelain crab *Petrolisthes cinctipes* by amino acids and sugars. *Comparative Biochemistry and Physiology*. 56A:19-22.
8. HARVEY, A., C. B. BOYKO, P. MCLAUGHLIN, AND J. W. MARTINS. 2014. *Anomura*, p. 284-295. *In: Atlas of crustacean larvae*. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
9. JENSEN, G. C. 1989. Gregarious settlement by megalopae of the porcelain crabs *Petrolisthes cinctipes* (Randall) and *Petrolisthes eriomerus* (Stimpson). *Journal of Experimental Marine Biology and Ecology*. 131:223-231.
10. JENSEN, G. C. 1991. Competence, settling behavior, and post-settlement aggregation by porcelain crab megalopae (*Anomura*, *Porcellanidae*). *Journal of Experimental Marine Biology and Ecology*. 153:49-61.
11. JENSEN, G. C., AND D. A. ARMSTRONG. 1991. Intertidal zonation among congeners: factors regulating distribution of porcelain crabs *Petrolisthes* spp. (*Anomura*, *Porcellanidae*). *Marine Ecology Progress Series*. 73:47-60.
12. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
13. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, AND E. CAMPOS. 2007. *Decapoda*, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
14. KURUP, N. G. 1964a. The incretory organs of the eye-stalk and brain of the porcelain crab, *Petrolisthes cinctipes* (Randall) (*Reptantia*, *Anomura*). *General and Comparative Endocrinology*. 4:99-112.
15. KURUP, N. G. 1964b. The intermolt cycle of an anomuran, *Petrolisthes cinctipes* (Randall) (*Crustacea*, *Decapoda*). *Biological Bulletin*. 127:97-107.
16. MACE, A. J., AND S. G. MORGAN. 2006. Biological and physical coupling in the lee of a small headland: contrasting transport mechanisms for crab larvae in an upwelling region. *Marine Ecology Progress Series*. 324:185-196.
17. MACGINITIE, G. E., AND N. MACGINITIE. 1949. *Natural history of marine animals*. McGraw-Hill Book Co., New York.
18. MILLER, S. H., AND S. G. MORGAN. 2013. Interspecific differences in depth preference: regulation of larval transport in an upwelling system.

- Marine Ecology Progress Series. 476:301-306.
19. PAGANINI, A. W., N. A. MILLER, AND J. H. STILLMAN. 2014. Temperature and acidification variability reduce physiological performance in the intertidal zone porcelain crab *Petrolisthes cinctipes*. *Journal of Experimental Biology*. 217:3974-3980.
 20. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 21. RICKETTS, E. F., AND J. CALVIN. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
 22. RONGES, D., J. P. WALSH, B. J. SINCLAIR, AND J. H. STILLMAN. 2012. Changes in extreme cold tolerance, membrane composition and cardiac transcriptome during the first day of thermal acclimation in the porcelain crab *Petrolisthes cinctipes*. *Journal of Experimental Biology*. 215:1824-1836.
 23. RUPPERT, E. E., R. S. FOX, AND R. D. BARNES. 2004. Invertebrate zoology: a functional evolutionary approach. Thomson Brooks/Cole, Belmont, CA.
 24. SCHMITT, W. L. 1921. The marine decapod crustacea of California. University of California Publications in Zoology. 23:1-470.
 25. SHANKS, A. L. 2009. Pelagic larval duration and dispersal distance revisited. *Biological Bulletin*. 216:373-385.
 26. SOMERO, G. N. 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *Journal of Experimental Biology*. 213:912-920.
 27. STILLMAN, J. H., AND G. N. SOMERO. 2000. A comparative analysis of the upper thermal tolerance limits of eastern Pacific porcelain crabs, genus *Petrolisthes*: influences of latitude, vertical zonation, acclimation, and phylogeny. *Physiological and Biochemical Zoology*. 73:200-208.
 28. TOONEN, R. J. 2004. Genetic evidence of multiple paternity of broods in the intertidal crab *Petrolisthes cinctipes*. *Marine Ecology Progress Series*. 270:259-263.
 29. WASSON, K., AND B. E. LYON. 2005. Flight or fight: flexible anti-predatory strategies in porcelain crabs. *Behavioral Ecology*. 16:1037-1041.
 30. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

Upogebia pugettensis

The blue mud shrimp

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Anomura, Paguroidea
Family: Upogebiidae

Taxonomy: Dana described *Gebia pugettensis* in 1852 and this species was later redescribed as *Upogebia pugettensis* (Stevens 1928; Williams 1986).

Description

Size: The type specimen was 50.8 mm in length and the illustrated specimen (ovigerous female from Coos Bay, Fig. 1) was 90 mm in length. Individuals are often larger and reach sizes to 100 mm (range 75–112 mm) and northern specimens are larger than those in southern California (MacGinitie and MacGinitie 1949; Wicksten 2011).

Color: Light blue green to deep olive brown with brown fringes on pleopods and pleon. Individual color variable and may depend on feeding habits (see Fig. 321, Kozloff 1993; Wicksten 2011).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are outstretched and shrimp-like in Upogebiidae (Kuris et al. 2007). For morphology of *Upogebia* (see Fig. 2, Williams 1986) and *U. pugettensis* see Williams (see Fig. 13, 1986).

Cephalothorax:

Eyes: Peduncle cylindrical (Schmitt 1921), eyestalks short but exceeding lateral rostral process. Corneas terminal and directed antero-laterally (Williams 1986).

Antennae: First segment of antennular peduncle has a sharp tooth at ventral border and second segment of flagellum has small, round disto-ventral spine (Wicksten 2011).

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to

the mouth and extend to cover the mandibles (Ruppert et al. 2004).

Carapace: Bears two rows of 11–12 teeth laterally (Fig. 1) in addition to a small distal spines (13 distal spines, 20 lateral teeth on carapace shoulder, see Wicksten 2011). Carapace with thalassinidean line extending from anterior to posterior margin (Wicksten 2011).

Rostrum: Large, tridentate, obtuse, rough and hairy (Schmitt 1921), the sides bear 3–5 short conical teeth (Wicksten 2011). Rostral tip shorter than antennular peduncle. Two short processes extending on either side each with 0–2 dorsal teeth (Wicksten 2011).

Teeth:

Pereopods: Two to five simple walking legs. Second pereopod is not chelate and bears setae on lower segment margins. Carpus has small spines and merus has a single small spine. Pereopods 3–5 setose, decrease progressively in size and have dactyls with spinules (Wicksten 2011).

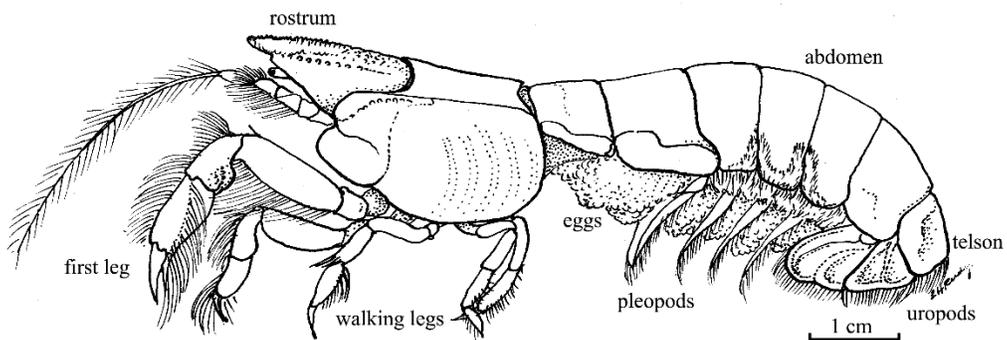
Chelipeds: First chelipeds approximately equal and subchelate (Fig. 1). Dactyls curved, with ridged upper surface and lateral surface with many tubercles (Wicksten 2011). Fixed finger slender (Williams 1986), with one conical tooth. Palm with setose lines, bearing setae and small teeth, as well as a sharp spine at dactyl base. Carpus with lateral and longitudinal furrow and spine with small teeth (4–10), two distal spines and, a larger marginal spine. The upper margin of the merus is curved and bears spines and small teeth (5–6). Ischium bears a single small spine (Wicksten 2011).

Abdomen (Pleon): Abdomen elongate and broad, not reflexed, extended, symmetrical and externally segmented. Bears four pairs of fan-like pleopods (Fig. 1).

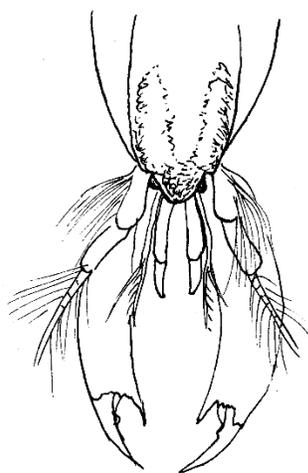
Telson & Uropods: Telson wide anteriorly and uropod length exceeds that of the telson. Uropods bear dorsal ribs and marginal spines (Wicksten 2011). Fan-like tail formed by telson, uropods adapted for swimming.

Sexual Dimorphism: The first pleopod is absent in males and is slender, bi-articulating

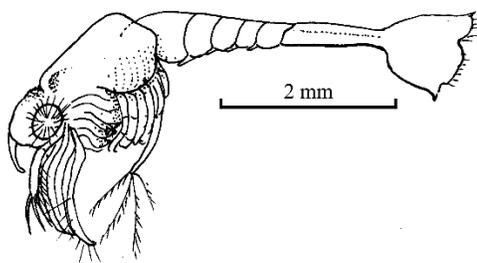
Upogebia pugettensis



1. *Upogebia pugettensis*, ovigerous ♀ x1 1/2:
actual size: 9 cm; first legs equal and
subchelate; legs 2,3,4,5 simple; four pairs of
fan-like pleopods.



2. Head (dorsal view):
hairy surface; rostrum: three
teeth, eyestalks cylindrical,
short; corneas terminal.



3. A larval form x15:
first stage, about 5 mm.

and simple in female *U. pugettensis* (Williams 1986).

Upogebiidae-specific Character

Burrow: *Upogebia pugettensis* builds U or Y-shaped burrows that are firm, permanent and simple with little branching (unlike *Neotrypaea californiensis*). Burrows extend vertically about 46 cm, then horizontally 0.6–1.2 m and up to the surface (MacGinitie 1930; Ricketts and Calvin 1971). Often, the entrance will have a gravel plug if the tide is out (Stevens 1928). The walls are smooth and mucus lined (MacGinitie and MacGinitie 1949). For figure see MacGinitie (1930).

Possible Misidentifications

Upogebiidae is described by Williams (1986) and Campos et al. (2009) and the single local species, *Upogebia pugettensis* (the blue mud shrimp) often co-occurs with *N. californiensis*. *Upogebia pugettensis* is easy to recognize because it is larger and its color (bluish and never red or pink) is strikingly different. Its burrows are also more firm and substantial. The most noticeable morphological difference between these species is the first pair of legs: both of which are small, sub-chelate and equal in *U. pugettensis*. Furthermore, its rostrum is hairy and has a laterally compressed and slender tip of the short fixed finger of the chela (Wicksten 2011).

Characteristics defining the Callianassidae are described by Sakai (1999) and Campos et al. (2009). There are three species locally, *Neotrypaea californiensis*, *N. gigas* and *N. biffari* (Kuris et al. 2007). *Neotrypaea californiensis* can be distinguished from the other two species by the lack of a prominent rostrum (present in *N. gigas*) and eyestalks that are acute and diverging tips of the eyestalks (rather than short, blunt and not diverging in *N. biffari*) (see Campos et al. 2009). *Neotrypaea gigas* is larger (to 125–150 mm) than the other two, and relatively rare in sandy sublittoral habitats. Its rostrum is sharp, with prominent medial tooth (not found in *N. californiensis*), and its first chela closes without a gap. It is more common in its southern distribution, south of Point Conception (Barnard et al. 1980; Kuris et al. 2007; Wicksten 2011). *Neotrypaea gigas* and *N. californiensis* also differ in the morphology of the second pereopod: In *N. californiensis* the propodus

and dactyl are of equal length and in *N. gigas*, the propodus is curved and wider than the dactyl (Kuris et al. 2007). Recent examination of these two species using morphological and molecular data suggests that the key characters for differentiating species is the length of eyestalks and shape of the distal outer edges (Pernet et al. 2010).

Ecological Information

Range: Type locality is Puget Sound, Washington. Known range includes Alaska to Morrow Bay, California (see Fig. 1, Williams 1986; Wicksten 2011). Southern populations of *U. pugettensis* become replaced by the congener, *U. macginitieorum* (Kuris et al. 2007).

Local Distribution: Oregon estuaries and sloughs including Alsea, Nestucca, Netarts, Yaquina, Coos Bay.

Habitat: Estuarine mudflats (in areas without *Zostera*, Stevens 1928), in mud or sandy mud, often with some gravel. In adaptation to living in an environment that is relatively low in oxygen, *N. californiensis* and *U.*

pugettensis exhibit low metabolic rates and can both survive periods of anoxia. *Upogebia pugettensis* has a higher metabolic rate and cannot survive periods of anoxia as well as *N. californiensis* (Thompson and Pritchard 1969a; Barnard et al. 1980; Zebe 1982).

Salinity: Collected at salinities of 30. A strong hyperosmotic regulator, their lower lethal limit is 3.5 (Thompson and Pritchard 1969b; Barnard et al. 1980).

Temperature:

Tidal Level: Intertidal to shallow subtidal, near shore (Wicksten 2011). Mid to lower intertidal of bays (Stevens 1928; Kuris et al. 2007) and usually lower than *N. californiensis*. Occasionally small individuals occur quite high in the intertidal (Ricketts and Calvin 1971).

Associates: The blue mud shrimp, *Upogebia pugettensis*, is found overlapping the range of *N. californiensis*, though it is generally found in lower intertidal burrows and in muddier sediments. Common commensals in ghost shrimp burrows include a polynoid worm *Hesperonoe*, pinnotherid crabs (*Scleroplax glanulata*), copepods (*Hemicyclops*, *Clausidium*), the shrimp *Betaeus harrimani*, the bopyrid isopod *Ione cornuta*, the goby *Clevelandia*, the echiuroid worm *Urechis caupo*, and the clam *Cryptomya californica*

(MacGinitie 1934; Kuris et al. 2007; Campos et al. 2009; Wicksten 2011). The parasitic bopyrid isopod, *Orthione griffenis*, was introduced to the Pacific coast from Asia in the 1980s and is thought to have caused the 2002 collapse of *U. pugettensis* on the Pacific coast (e.g. Willapa Bay, Washington, see Fig. 1, Dumbauld et al. 2011; Williams and Boyko 2012). This parasite was discovered in Yaquina Bay, Oregon in 1999 and was the first parasite known from the gills of *Upogebia* in western North America (Markham 2004; Chapman et al. 2012). Larvae of the commensal phoronid, *Phoronis pallida*, exhibit increased swimming speed and settlement behavior in the presence of *Upogebia*-conditioned seawater (Santagata 2004).

Abundance: Can be locally common (Kuris et al. 2007). In Willapa Bay, Washington, the density of *N. californiensis* (up to 450 shrimp per m²) was always higher than that of the other locally occurring ghost shrimp, *U. pugettensis* (up to 100 shrimp per m²) (Dumbauld et al. 1996).

Life-History Information

Reproduction: Each burrow inhabited by one pair (Barnard et al. 1980). Oviparous females found December and February (Elkhorn Slough California, MacGinitie and MacGinitie 1949), October through May (Willapa Bay, Washington, Dumbauld et al. 1996) and early April (South Slough, Coos Bay, Oregon). Eggs carried under abdomen on pleopods (Fig. 2). *Neotrypaea californiensis* reach sexual maturity at 2 years and produce 3,900 eggs while *U. pugettensis* produces 7,100 (Dumbauld et al. 1996).

Larva: The larvae of *U. pugettensis* are found in plankton samples from February to June and their morphology was described by Hart (1937). Larval development in *U. pugettensis* proceeds via three zoea stages and, a final megalopa stage, each marked by a molt (Hart 1937; Puls 2001). *Upogebia pugettensis* zoea have rostrum shorter than antennules (1/3 antennule length, compare to Callianassidae), five abdominal segments, swimming setae on exopods and maxillipeds, and triangular telson with indentation at posterior margin with five setae, unlike *N. californiensis*, which have a medial tooth at telson posterior (see paguroid zoeae Fig. 53.2, Harvey et al. 2014; Hart 1937; Puls 2001). Larval size (measured from tip of

rostrum to tip of telson) proceeds from 3.7 mm (Zoea I, Fig. 3), to 4.4 mm (Zoea II), to 5.4 mm (Zoea III) (Puls 2001). Megalopae are shrimp-like in morphology with blunt rostrum, pereopods and maxillipeds resembling adults. The telson becomes rectangular and has rounded uropods laterally. Pleopods on abdominal segments 2–5 have setae (Puls 2001). *Upogebia pugettensis* larvae recruit in spring (April–June) (Willapa Bay, Washington, Dumbauld et al. 1996).

Juvenile: Sexual dimorphism occurs before maturation in *U. pugettensis* (unlike *N. californiensis*), where claw size occurs almost immediately (<1 year old), when individuals are 4–5 mm in (carapace) length (Dumbauld et al. 1996).

Longevity: Moderately long lived (Ricketts and Calvin 1971).

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007). The growth rate for *U. pugettensis* is approximately 4–5 mm (carapace length) per year (Dumbauld et al. 1996).

Food: Detritivore, obtaining food by filtering water through the burrow as it sits near the entrance. Individuals make a “basket” (MacGinitie 1930) with its first and second pereopods, which have long setae. Griffen et al. (2004) estimated filtration rates for *U. pugettensis* and its commensal bivalve *Cryptomya californica* at three phytoplankton densities (low, medium and high).. They found that *U. pugettensis* removed 57, 53 and 40% of phytoplankton drawn into the burrow, while *C. californica* removed 12, 19 and 39%, respectively.

Predators: Adults are used by humans for fish bait, individuals avoid predation by retreating to burrow. Juveniles and larvae are eaten in the plankton (e.g. fish).

Behavior: Ghost shrimp species (*Neotrypaea*, *Upogebia*) are known to be ecosystem engineers with the ability to regulate and change community (macro and microbial communities) structure by burrowing

and deposit feeding (Dumbauld and Wyllie-Echeverria 2003; Bertics and Ziebis 2009). Their presence and behavior effects biogeochemical composition including sediment grain size, nutrient exchange (D'Andrea and DeWitt 2009) and organic composition. Bioturbation (Kristensen et al. 2012) turns over and re-suspends sediment, which can increase erosion and sediment instability, having a negative effect on algae and seagrasses that require light for photosynthesis (e.g. *Zostera*, Dumbauld and Wyllie-Echeverria 2003) and suspension feeders (e.g. oysters, Dumbauld et al. 1996). In turn, seagrasses tend to solidify sediment and are not suitable habitats for ghost shrimp species (Berkenbusch et al. 2007). In controlled experiments, the presence of *U. pugettensis* lowers abundances of other estuarine crustaceans and polychaetes (Posey et al. 1991).

Bibliography

1. BARNARD, L. J., D. E. BOWERS, AND E. C. HADERLIE. 1980. Macrura and Anomura, p. 577-593. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
2. BERKENBUSCH, K., A. A. ROWDEN, AND T. E. MYERS. 2007. Interactions between seagrasses and burrowing ghost shrimps and their influence on infaunal assemblages. *Journal of Experimental Marine Biology and Ecology*. 341:70-84.
3. BERTICS, V. J., AND W. ZIEBIS. 2009. Biodiversity of benthic microbial communities in bioturbated coastal sediments is controlled by geochemical microniches. *Isme Journal*. 3:1269-1285.
4. CAMPOS, E., A. R. DE CAMPOS, AND I. MANRIQUEZ. 2009. Intertidal thalassinidean shrimps (Thalassinidea, Callianassidae and Upogebiidae) of the west coast of Baja, California, Mexico: annotated checklist, key for identification, and symbionts. *Crustaceana*. 82:1249-1263.
5. CHAPMAN, J. W., B. R. DUMBAULD, G. ITANI, AND J. C. MARKHAM. 2012. An introduced Asian parasite threatens northeastern Pacific estuarine ecosystems. *Biological Invasions*. 14:1221-1236.
6. D'ANDREA, A. F., AND T. H. DEWITT. 2009. Geochemical ecosystem engineering by the mud shrimp *Upogebia pugettensis* (Crustacea: Thalassinidae) in Yaquina Bay, Oregon: Density-dependent effects on organic matter remineralization and nutrient cycling. *Limnology and Oceanography*. 54:1911-1932.
7. DUMBAULD, B. R., D. A. ARMSTRONG, AND K. L. FELDMAN. 1996. Life-history characteristics of two sympatric thalassinidean shrimps, *Neotrypaea californiensis* and *Upogebia pugettensis*, with implications for oyster culture. *Journal of Crustacean Biology*. 16:689-708.
8. DUMBAULD, B. R., J. W. CHAPMAN, M. E. TORCHIN, AND A. M. KURIS. 2011. Is the collapse of mud shrimp (*Upogebia pugettensis*) populations along the Pacific coast of North America caused by outbreaks of a previously unknown bopyrid isopod parasite (*Orthione griffenis*)? *Estuaries and Coasts*. 34:336-350.
9. DUMBAULD, B. R., AND S. WYLLIE-ECHEVERRIA. 2003. The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. *Aquatic Botany*. 77:27-42.
10. GRIFFEN, B. D., T. H. DEWITT, AND C. LANGDON. 2004. Particle removal rates by the mud shrimp *Upogebia pugettensis*, its burrow, and a commensal clam: effects on estuarine phytoplankton abundance. *Marine Ecology Progress Series*. 269:223-236.
11. HART, J. F. L. 1937. Larval and adult stages of British Columbian anomura. *Canadian Journal of Research (D)*. 15:179-220.
12. HARVEY, A. W., C. B. BOYKO, P. MCLAUGHLIN, AND J. W. MARTINS. 2014. Anomura, p. 284-295. *In: Atlas of crustacean larvae*. J. W. Martin, J.

- Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
13. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
 14. KRISTENSEN, E., G. PENHA-LOPES, M. DELEFOSSE, T. VALDEMARSEN, C. O. QUINTANA, AND G. T. BANTA. 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series*. 446:285-302.
 15. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, AND E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 16. MACGINITIE, G. E. 1930. The natural history of the mud shrimp *Upogebia pugettensis* (Dana). *Annals and Magazine of Natural History*. London. 10:36-44.
 17. MACGINITIE, G. E., AND N. MACGINITIE. 1949. *Natural history of marine animals*. McGraw-Hill Book Co., New York.
 18. MARKHAM, J. C. 2004. New species and records of Bopyridae (Crustacea, Isopoda) infesting species of the genus *Upogebia* (Crustacea, Decapoda, Upogebiidae): the genera *Orthione* Markham, 1988, and *Gyge* Cornalia & Panceri, 1861. *Proceedings of the Biological Society of Washington*. 117:186-198.
 19. PERNET, B., A. DECONINCK, AND L. HANEY. 2010. Molecular and morphological markers for distinguishing the sympatric intertidal ghost shrimp *Neotrypaea californiensis* and *N. gigas* in the eastern Pacific. *Journal of Crustacean Biology*. 30:323-331.
 20. POSEY, M. H., B. R. DUMBAULD, AND D. A. ARMSTRONG. 1991. Effects of a burrowing mud shrimp, *Upogebia pugettensis* (Dana,) on abundances of macro-infauna. *Journal of Experimental Marine Biology and Ecology*. 148:283-294.
 21. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 22. RICKETTS, E. F., AND J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 23. RUPPERT, E. E., R. S. FOX, AND R. D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*. Thomson Brooks/Cole, Belmont, CA.
 24. SAKAI, K. 1999. Synopsis of the family Callianassidae, with keys to subfamilies, genera and species, and the description of new taxa (Crustacea: Decapoda: Thalassinidea). Nationaal Natuurhistorisch Museum, Leiden, Netherlands.
 25. SANTAGATA, S. 2004. A waterborne behavioral cue for the actinotroch larva of *Phoronis pallida* (Phoronida) produced by *Upogebia pugettensis* (Decapoda, Thalassinidea). *Biological Bulletin*. 207:103-115.
 26. SCHMITT, W. L. 1921. The marine decapod crustacea of California. *University of California Publications in Zoology*. 23:1-470.
 27. STEVENS, B. A. 1928. Callianassidae from the west coast of North America. *Publications of the Puget Sound Biological Station*. 6:315-369.
 28. THOMPSON, J. L., AND A. W. PRITCHARD. 1969. Osmoregulatory capabilities of *Callianassa* and *Upogebia* (Crustacea: Thalassinidea). *Biological Bulletin*. 136:114-129.
 29. THOMPSON, R. K., AND A. W. PRITCHARD. 1969. Respiratory adaptation of two burrowing crustaceans *Callianassa californiensis* and *Upogebia pugettensis* (Decapoda, Thalassinidea). *Biological Bulletin*. 136:274-287.
 30. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

31. WILLIAMS, A. B. 1986. Mud shrimps *Upogebia* from the eastern Pacific: *Thalassinidea upogebiidae*. San Diego Society of Natural History Memoirs:1-60.
32. WILLIAMS, J. D., AND C. B. BOYKO. 2012. The Global diversity of parasitic isopods associated with crustacean hosts (Isopoda: Bopyroidea and Cryptoniscoidea). PLoS ONE. 7:e35350.
33. ZEBE, E. 1982. Anaerobic metabolism in *Upogebia pugettensis* and *Callinassa californiensis* (Crustacea, Thalassinidea). Comparative Biochemistry and Physiology B-Biochemistry & Molecular Biology. 72:613-617.

Updated 2015

Cancer antennarius

Pacific rock crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Brachyura
Family: Cancridae

Taxonomy: The most recent taxonomic debate regards this species being placed in the recently elevated genus, *Romaleon* (Schweitzer and Feldmann 2000). However, molecular work does not always support the monophyly of this or other cancrid genera (Harrison and Crespi 1999). Although many researchers have switched to the name *R. antennarius* (or *R. antennarium*) (e.g., Wicksten 2011), we follow the most current local intertidal guide that retains the name *Cancer antennarius* (Kuris et al. 2007).

Description

Size: Females up to 148 mm in carapace width and males 178 mm (Puls 2001). Type specimen carapace is 118 mm in width (Rathbun 1930).

Color: Reddish color dorsally, light yellow ventrally with red spots, especially frontally (Ricketts and Calvin 1971). Chelae dactyls dark (Wicksten 2011) (Fig. 1).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are reduced and folded ventrally (Decapoda, Kuris et al. 2007).

Cephalothorax:

Eyes: Eyestalks short, orbits small. Eyes are frontal with a small supra-orbital tooth (Fig. 1).

Antennae:

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004). Merus of third maxillipeds with distal margin and rounded angles in *C. antennarius* (Wicksten 2011).

Carapace: Oval and widest at eighth tooth. Antero-lateral and postero-lateral margins meet at distinct angle. Carapace surface lumpy, uneven and finely granulated (Fig. 1).

Frontal Area: Frontal area not produced with five medial (three central) teeth, of which the outer pair is the largest, center tooth small (Fig. 2) (Kuris et al. 2007; Wicksten 2011).

Teeth: 11 antero- and post-lateral teeth are curved forward (Fig. 2).

Pereopods: Walking legs rough and hairy. Dactyls with five longitudinal rows of bristles (Rathbun 1930).

Chelipeds: Chelae heavy, nearly smooth and black-tipped. Inner carpus (wrist) with single sharp spine. Chelipeds can be slightly unequal in size (Wicksten 2011).

Abdomen (Pleon): Abdomen narrow in male, broad in female (e.g. see *Cancer magister*, Fig. 3).

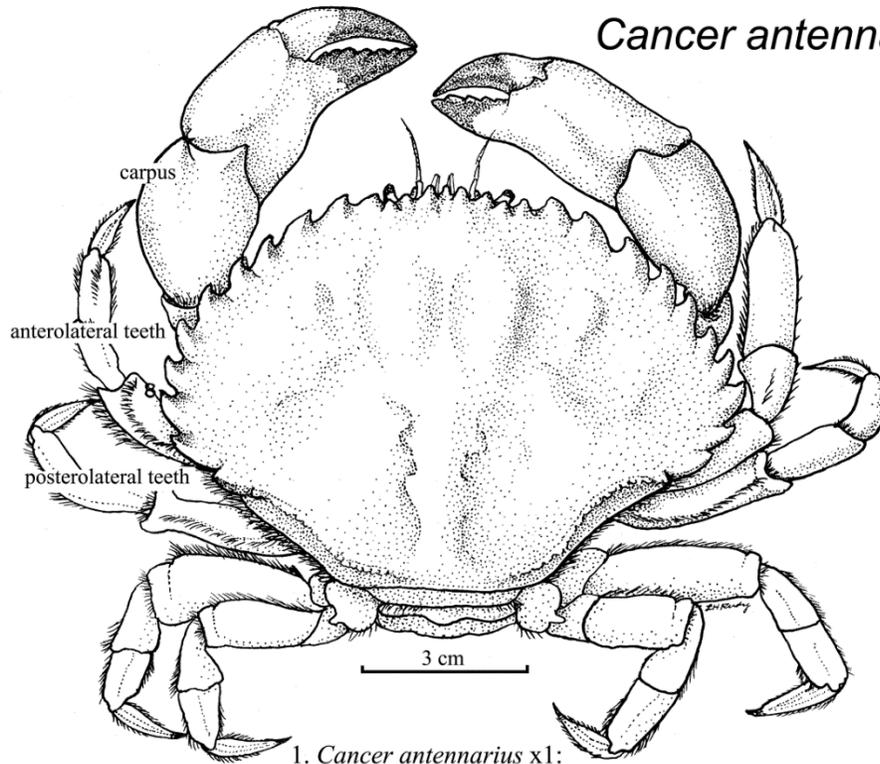
Telson & Uropods:

Sexual Dimorphism: Male and female brachyuran crabs are easily differentiated. The most conspicuous feature, the abdomen, is narrow and triangular in males while it is wide and flap-like in females. Additionally, males have one large chelae and two pleopod pairs specialized for copulation however, the third and fourth pleopods are absent. Females, on the other hand, have all four pleopod pairs, each with long setae for egg attachment (Brachyura, Kuris et al. 2007).

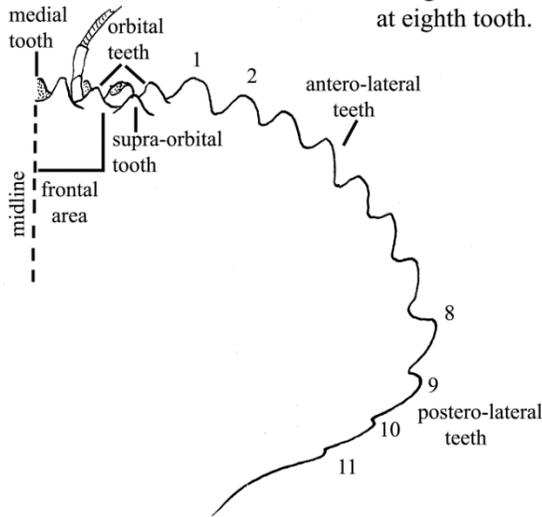
Possible Misidentifications

According to some authors, the genus *Cancer* comprises 23 species (Harrison and Crespi 1999 but see Schweitzer and Feldmann 2000). This genus is differentiated from other brachyuran genera by the broadly oval carapace, presence of five frontal teeth and antennules that fold back over carapace. Characters unique to *Cancer antennarius* include 11 antero-lateral teeth, carapace widest at 8 tooth, red color, black-tipped cheliped dactyls and small size (Kuris et al. 2007). *Cancer antennarius* is

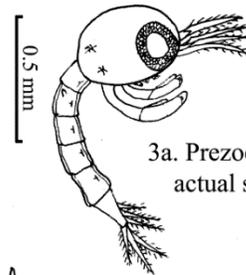
Cancer antennarius



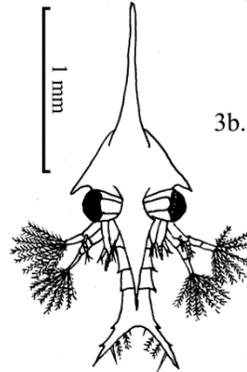
1. *Cancer antennarius* x1:
actual size 10 cm; dark red;
black tipped claws; red spots
on light underbody; widest
at eighth tooth.



2. Carapace (right front)
eleven antero- and post-
lateral teeth; frontal area
not produced; eyes small,
frontal; supra-orbital tooth;
small medial tooth (below).



3a. Prezoea x45:
actual size 1.65 mm.



3b. Third zoea x30:
actual size 2.25 mm
(from Roesijadi, 1976).

smaller than most of the other adult *Cancer* species. In color, *C. productus* is most similar to *C. antennarius* (dark red, black-tipped chelae), but never has red spots on its underbody, though its legs may be mottled. They also occur in the same ecological niches. Furthermore, *C. productus* has ten teeth (not 11). *Cancer antennarius* is also smaller than *C. productus*, and lacks its obviously pronounced frontal area.

There are eight *Cancer* species known locally (Kuris et al. 2007). *Cancer magister* (adults at least 30 mm in width), *C. productus* (adults over 20 mm in width) and *C. antennarius* (adults typically 100 mm in width) are the largest species. *Cancer productus* and *C. magister* have 10 antero-lateral teeth and five subequal frontal teeth (Kuris et al. 2007). The carapace of *C. magister* is widest at the tenth tooth, is more subtly pigmented and does not have black tipped dactyls seen in *C. productus* (Schmitt 1921; Kuris et al. 2007; Wicksten 2011).

The remaining four species tend to be smaller and have nine antero-lateral teeth (sometimes ten in older specimens, Wicksten 2011). *Cancer branneri* is a small species (35 mm) that is rare intertidally and recognizable by cheliped dactyls that are long, straight, black and spiny. *Cancer gracilis* (27 mm) has white-tipped cheliped dactyls and *C. jordani* (25 mm) has a hairy carapace and sharp curving teeth. *Cancer anthonyi*, the yellow rock crab, is larger than the previous three at 52 mm and has black-tipped cheliped dactyls (Kuris et al. 2007; Wicksten 2011). Populations of *C. productus*, *C. anthonyi* (southern California) and *C. magister* support commercial fisheries (Kuris et al. 2007). *Cancer antennarius* is a common species used in biochemistry and physiology studies (e.g. Spaziani et al. 1997; Kang and Spaziani 1996; Rudolph and Spaziani 1991).

Ecological Information

Range: Type locality is San Francisco. Known range includes British Columbia, Canada to Baja, California. Not common in Puget Sound.

Local Distribution: In Coos Bay (and probably other Oregon estuaries) individuals are most common on protected outer coast.

Habitat: Often buried in the sand and under rocks (Ricketts and Calvin 1971).

Salinity: In San Francisco, found at salinities ranging from 26.6 to 33.3 (Schmitt 1921).

Cancer antennarius cannot tolerate brackish conditions and cannot osmoregulate (Garth and Abbott 1980).

Temperature: In San Francisco Bay, individuals collected at 8.7–14.3° C (Schmitt 1921).

Tidal Level: Occurs in lower tide pools (Ricketts and Calvin 1971) and subtidally to 91 m (Kittredge et al. 1971; Puls 2001).

Associates: Often encrusted with polychaetes (family Iphitimidae) in branchial cavities (southern California) (Kuris et al. 2007).

Abundance: Common in California and Oregon, becomes rarer farther north.

Life-History Information

Reproduction: Mating occurs when the female is about to molt, male *C. antennarius* clasp females several days prior to molting and copulation takes place after molting occurs. In the lab, males were stimulated to pre-mating behavior by the release of a molting hormone by *Pachygrapsus crassipes* (Kittredge et al. 1971). Fertilization is internal, occurs after molting and egg deposition occurs months later (November–January, Ricketts and Calvin 1971). Females with eggs were encountered in Humboldt Bay, California in April (Puls 2001). All decapod crustacean females attach recently laid gelatinous egg masses to their pleopods. The outer embryo membrane thickens and a strand develops that attaches each embryo to pleopod setae (Decapoda, Kuris et al. 2007).

Larva: The larvae of *C. antennarius* were described by Roesijadi (1976). Larval development proceeds via a series of zoea (five total, telson with single lateral spine at each fork, Lough 1975) and megalopae stages, each marked by a molt (Roesijadi 1976). *Cancer antennarius* zoea are planktotrophic and have large compound eyes and four spines: one each dorsal and rostral and two lateral (Fig. 3b) (see Fig. 4, Roesijadi 1976; Puls 2001; Martin 2014). Larval size (measured from tip of rostrum to tip of telson) proceeds from 1.8 mm (Zoea I) to 4.4 mm (Zoea V) (Puls 2001). Megalopae are 2.3–3.3 mm from rostrum tip to posterior carapace and 1.4–2.4 mm in width. The megalopae bear one stout spine on ischiopodite of cheliped and exhibit similar

morphology to the larvae of *C. gracilis* (Puls 2001). The larvae of cancrid species are difficult to distinguish, especially the prezoal stages (Fig. 3a), but the zoea and megalopae of *C. antennarius* are smaller and possess fewer setae than other species. In larvae reared at 13.8°C, hatching from the fifth zoeal stage to the megalopa occurred at 36 days, which is shorter than observed for *C. magister* or *C. productus* (Roesijadi 1976).

Juvenile: Juvenile *C. antennarius* may have second small spine on carpus. Their carapace is widest at the ninth tooth, the tenth (and last) tooth is prominent and shiny. Carapace is crowded with granules. The manus of cheliped are light in color, fingers (dactyls) bear dark pigment and extreme tips are light in color. Legs may bear more setae than is seen in adult individuals (Wicksten 2011).

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: A scavenger and predator, particularly of hermit crabs (Garth and Abbott 1980).

Predators: Octopuses, sea otters and occasionally harvested by sport fishermen. Larvae are preyed upon by plankton feeders (herring, salmon, etc.).

Behavior:

Bibliography

1. GARTH, J. S., and D. P. ABBOTT. 1980. Brachyura: the true crabs, p. 594-630. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
2. HARRISON, M. K., and B. J. CRESPI. 1999. Phylogenetics of Cancer crabs (Crustacea : Decapoda : Brachyura). *Molecular Phylogenetics and Evolution*. 12:186-199.
3. KANG, B. K., and E. SPAZIANI. 1996. Uptake of high-density lipoprotein by Y-organs of the crab, *Cancer antennarius*. 1. Characterization in vitro and effects of stimulators and inhibitors. *Archives of Insect Biochemistry and Physiology*. 31:106-106.
4. KITTREDGE, J. S., M. TERRY, and F. T. TAKAHASHI. 1971. Sex pheromone activity of the molting hormone, crustecdysone, on male crabs (*Pachygrapsus crassipes*, *Cancer antennarius*, and *C. anthonyi*). *Fishery Bulletin*. 69:337-343.
5. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
6. LOUGH, R. G. 1975. Dynamics of crab larvae (Anomura: Brachyura) off the central Oregon coast, 1969-1971. Ph.D. Oregon State University, Corvallis, OR.
7. MARTIN, J. W. 2014. Brachyura, p. 295-310. *In: Atlas of crustacean larvae*. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
8. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
9. RATHBUN, M. J. 1930. The Cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. U.S. Government Printing Office, Washington, D.C.
10. RICKETTS, E. F., and J. CALVIN. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
11. ROESIJADI, G. 1976. Descriptions of the prezoae of *Cancer magister* Dana and *Cancer productus* Randall and the larval stages of *Cancer antennarius* Stimpson (Decapoda: Brachyura). *Crustaceana*. 31:275-295.
12. RUDOLPH, P. H., and E. SPAZIANI. 1991. Neurons demonstrable by nickle lysine backfilling of the optic peduncle in the crab *Cancer antennarius*. *Comparative Biochemistry and*

- Physiology C-Pharmacology
Toxicology & Endocrinology. 99:179-184.
13. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. Invertebrate zoology: a functional evolutionary approach. Thomson Brooks/Cole, Belmont, CA.
 14. SCHMITT, W. L. 1921. The marine decapod crustacea of California. University of California Publications in Zoology. 23:1-470.
 15. SCHWEITZER, C. E., and R. M. FELDMANN. 2000. Re-evaluation of the Cancridae Latreille, 1802 (Decapoda: Brachyura) including three new genera and three new species. Contributions to Zoology. 69:223-250.
 16. SPAZIANI, E., K. DESANTIS, B. D. OROURKE, W. L. WANG, and J. D. WELD. 1997. The clearance in vivo and metabolism of ecdysone and 3-dehydroecdysone in tissues of the crab *Cancer antennarius*. Journal of Experimental Zoology. 279:609-619.
 17. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

Cancer magister

Dungeness or market crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Brachyura
Family: Cancridae

Taxonomy: Recent morphological studies have elevated the subgenus *Metacarcinus* to genus level (Schweitzer and Feldmann 2000). However, molecular work does not always support the monophyly of this or other cancrinid genera (Harrison and Crespi 1999). Although many researchers have switched to the name *Metacarcinus magister* (e.g. Wicksten 2011; Rasmuson and Shanks 2014; Dunn and Young 2014), we follow current local intertidal guides and reviews of the species that retain the name *Cancer magister* (e.g. Kuris et al. 2007; Rasmuson 2013).

Description

Size: Carapace 120.7 mm in length, 177.8 mm in width. Up to 1.36 kg in weight, though average weight of four-year old (i.e. fully mature) males is 0.91 kg (Rasmuson 2013).

Color: Light reddish brown, darkest anteriorly, often light orange below (Rathbun 1930), sometimes with gray-purple mottling dorsally. Inner sides of anterior dactyls and propodi crimson, but tips not darkly pigmented (Rathbun 1930; Kuris et al. 2007).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are reduced and folded ventrally (Decapoda, Kuris et al. 2007).

Cephalothorax:

Eyes: Eyestalks short, orbits small.

Antennae: Antennules folded lengthwise and antennal flagella short and, more or less, hairy (Rathbun 1930).

Mouthparts: The mouth of decapod crustaceans is comprised of six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004).

Carapace: Broadly oval, uneven but not highly sculptured and with granular texture. Carapace width greatest at tenth tooth (Fig. 1). Postero-lateral margin is unbroken, entire and without teeth. The antero-lateral margin meets the postero-lateral margin with distinct angle (Fig. 1).

Frontal Area: No rostrum. Narrow and with five unequal teeth, not markedly produced beyond outer orbital angles. Middle tooth largest and more advanced than outer pair. The outer pair form inner orbital angles (Fig. 2).

Teeth: Ten antero-lateral teeth, counting the orbital tooth. All teeth are pointed and with anterior serrations. The tenth tooth is large and projecting.

Pereopods: Rough above, broad and flat (especially the propodus and dactylus of last pair).

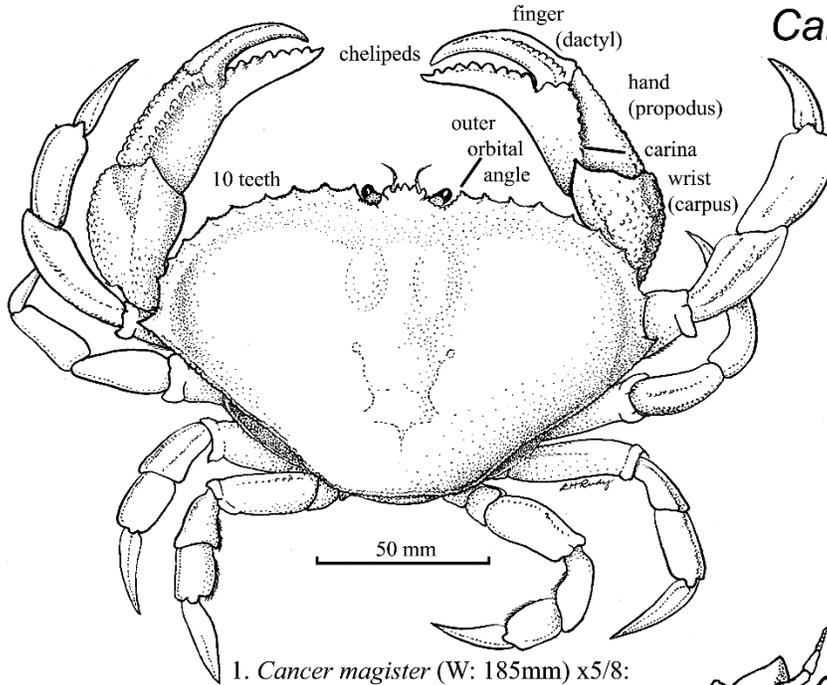
Chelipeds: Dactyls not pigmented and dactyl spines on upper surface. The fixed finger is much deflexed. The hand (propodus) has six carineae on upper outer surface and the wrist (carpus) has a strong inner spine (Fig. 1).

Abdomen (Pleon): Abdomen narrow in male, broad in female (Fig. 3).

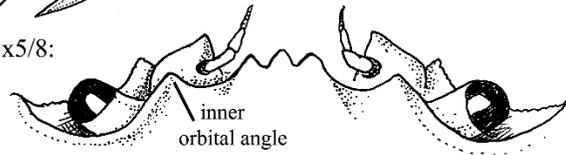
Telson & Uropods: One feature that may be taxonomically relevant to the placement of this species within *Metacarcinus* or *Cancer* (see **taxonomy**) is the telson morphology. The genus *Metacarcinus* is characterized by males with a rounded tip to the telson, while the males of *Cancer* species have a more sharply pointed telson tip (Schram and Ng 2012).

Sexual Dimorphism: Male and female brachyuran crabs are easily differentiable. The most conspicuous feature, the abdomen, is narrow and triangular in males while it is wide and flap-like in females (Fig. 3). Additionally, males have one large chelae and two pleopod pairs specialized for copulation, however, the third and fourth pleopods are absent. Females, on the other hand, have all four pleopod pairs, each with long setae for

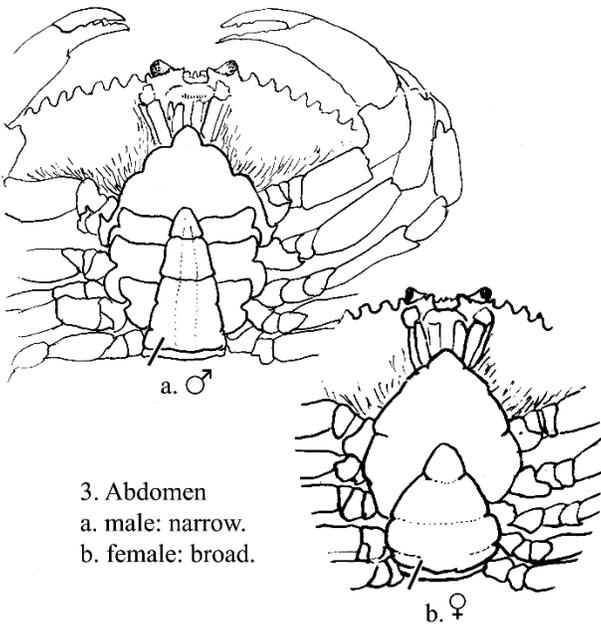
Cancer magister



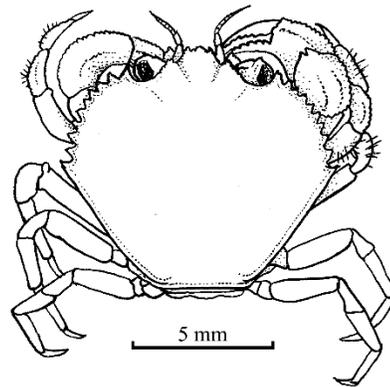
1. *Cancer magister* (W: 185mm) x5/8:
 ten antero-lateral teeth;
 postero-lateral margin entire;
 front: five unequal teeth;
 carapace: broadly oval, widest at
 tenth tooth; fingers light.



2. Front:
 not markedly pronounced; middle
 tooth largest, most advanced;
 outer pair form inner orbital angles.



3. Abdomen
 a. male: narrow.
 b. female: broad.



4. Juvenile (W: 10mm) x5:
 carapace rectangular; ten
 teeth; fingers light.

egg attachment (Brachyura, Kuris et al. 2007).

Possible Misidentifications

According to some authors, the genus *Cancer* comprises 23 species (Harrison and Crespi 1999). This genus is differentiated from other brachyuran genera by the broadly oval carapace, presence of five frontal teeth and antennules that fold back over carapace. Characters unique to *Cancer magister* include 10 antero-lateral teeth, carapace widest at tenth tooth and the lack of black-tipped cheliped dactyls.

There are eight *Cancer* species known locally (Kuris et al. 2007). *Cancer productus*, the most morphologically similar to *C. magister*, also has 10 antero-lateral teeth and five subequal (but nearly equal) frontal teeth (Kuris et al. 2007). However, its cheliped dactyls are black tipped, its carapace is widest at the ninth tooth and its body color can be uniformly brick red (characters not observed in *C. magister*) (Wicksten 2011). *Cancer antennarius*, like *C. productus*, is dark red with spots ventrally and with black tipped chelae. However, the carapace width in *C. antennarius* is widest at the eighth tooth and there are a total of 11 antero-lateral teeth (Wicksten 2011). *Cancer oregonensis* is a small, oval crab with 12–13 total teeth. The remaining four species have nine antero-lateral teeth (sometimes ten in older specimens, Wicksten 2011). *Cancer branneri* is a small species (35 mm) that is rare intertidally and recognizable by cheliped dactyls that are long, straight, black and spiny. *Cancer gracilis* is also small (27 mm) has white-tipped cheliped dactyls and *C. jordani* (25 mm) has a hairy carapace and sharp curving teeth. *Cancer anthonyi*, the yellow rock crab, is larger than the previous three at 52 mm and has black-tipped cheliped dactyls (Kuris et al. 2007; Wicksten 2011). Populations of *C. productus*, *C. anthonyi* (southern California) and *C. magister* support commercial fisheries (Kuris et al. 2007). Due to the extensive commercial fishery for *C. magister* (Alaska to California) there are many extensive reviews on this species (e.g. Wild and Tasto 1983; Pauley et al. 1989; Rasmuson 2013)

Ecological Information

Range: Type locality is San Francisco Bay (Schmitt 1921). Known range includes Alaska to Monterey Bay, California (Ricketts and Calvin 1971).

Local Distribution: Most local northwest estuaries and offshore waters. Also near shore and within bays in summer months (Ricketts and Calvin 1971).

Habitat: Individuals are found in many substrates, from mud to sand, gravel and rock (Schmitt 1921). *Cancer magister* appears to prefer sand (Weymouth 1914) and mud with eelgrass in bays (Kozloff 1974). Juveniles and adults tend to bury themselves into soft sand (Jaffe et al. 1987; McGaw 2005). In particular, females must be buried 5–10 cm deep to attach embryos to their pleopods (Fisher and Wickham 1976).

Salinity: In Coos Bay, individuals were collected at salinities from 11–35 (Dunn and Young 2013). Juvenile crabs are more tolerant to low salinity (Hunter and Rudy 1975; Robinson and Potts 1979). Dunn and Young (2013) found that the salinity tolerance of adult crabs may provide them refuge from the nemertean egg predator that is more prevalent in areas of high salinity.

Temperature:

Tidal Level:

Associates: Both male and female *C. magister* are usually infested with the nemertean egg predator *Carcinonemertes errans* (Wickham 1979a, b; Dunn and Young 2013). These worms occur all over the body of adults, particularly near the joints or abdominal flap and are transferred from males to females during copulation where they, eventually move toward the egg mass. The life-cycle of this nemertean is dependent on and corresponds to that of *C. magister* (Kuris 1993).

Abundance: Commercial catch in Oregon is cyclic in nature and has ranged from a high of 15,112,000 kg (2006) to a low of 224,000 kg (1928) (Fig. 3.3, Rasmuson 2013). Population fluctuations appear to be driven by two factors: 1) Initially the population is recruitment limited and the number of returning megalopae directly correlates to adult population size (Shanks 2013); 2) The number of returning megalopae are correlated with the local timing of the spring transition, the phase of the Pacific Decadal Oscillation and the amount of upwelling during the

season's megalopae recruit. When the number of returning megalopae is high, it appears that the adult population is set by density dependent effects.

Life-History Information

Reproduction: When the female is about to molt (March–June, Oregon), male *C. magister* clasp females and copulation takes place over several days (Snow and Nielsen 1966; Rasmuson 2013). Fertilization is internal and occurs after molting and egg deposition occurs months later. Eggs are approximately 390–420 µm in diameter and females carry broods up to 2.5 million from October to December. Eyespots and chromatophores are easily visible in advanced embryos (80 days at 10°C, Jaffe et al. 1987; Kuris et al. 2007). The larval duration ranges from 89–143 days (average 130), hatching occurs between January and March with settlement between April and August in Oregon and Washington (Table 3.1, Rasmuson 2013). See Rasmuson 2013 (Fig. 3.2) for *C. magister* life cycle.

Larva: Larval development proceeds via a series of zoea (five total) and megalopae stages, each marked by a molt. *Cancer magister* zoea are planktotrophic and have large compound eyes and four spines: one each dorsal and rostral and two lateral (see Fig. 31, Puls 2001; Rasmuson 2013; Martin 2014). Larval size (measured from tip of rostrum to tip of telson) proceeds from 2.5 mm (Zoea I) to 9 mm (Zoea V) (Puls 2001). The zoea of cancrivora species are difficult to distinguish but the megalopae of *C. magister* are distinctly larger than other cancrivora species (up to 6.6 mm vs 3 mm) (Puls 2001). Larval duration is estimated to be 80–160 days at 10°C, where 25–30 days are spent as megalopae (Jaffe et al. 1987; Puls 2001). Larval forms occur in nearshore waters and progressively move offshore. They return to nearshore shelf waters, bays and estuaries for metamorphosis. It is a common misconception that the larvae must settle in estuaries and, in reality, most settle on the continental shelf (Rasmuson 2013).

Juvenile: As in adults, the antero-lateral and postero-lateral margins meet with a distinct angle. The carapace is widest at the tenth tooth and postero-lateral margin is entire. The carpus of each cheliped is with single spine and dactyls are not pigmented

(Rathbun 1930). The carapace of juveniles is not as broad as in adults (compare Figs. 1 and 4).

Longevity: Lifespan ranges from 7–10 years (Ricketts and Calvin 1971; Gutermuth 1989) however fishery-based mortality truncates the lifespan of male *C. magister* to approximately four years.

Growth Rate: The “first crab” stage is reached at 80 days, at 11 °C (Anderson 1978). Sexual maturity is reached at 1³/₄ years (Morris et al. 1980) and individuals fully mature at 4–5 years (Ricketts and Calvin 1971). Growth rates by age are as follows: males and females at age 1 yr are 30 mm; males and females at age 2 yr are 95 mm; at age 3 yr males are 150 mm and females are 120 mm; and males at age 4 yr are 175 mm. A characteristic of ecdysozoans is growth that is punctuated by molting (ecdysis). Pre-molting periods are defined by the separation of the epidermis from the old cuticle and the dramatic increase in epidermal cell growth. Post-molt periods are recognizable by individuals that have soft shells as the cuticle gradually hardens and deposits a thin membranous layer. Furthermore, decapods have the ability to regenerate limbs, which have been autotomized as necessary, at subsequent molts (Kuris et al. 2007).

Food: An opportunistic feeder. Bivalves appear to be the most important food though fish bones and crustaceans have been found in the guts of *C. magister* (Butler 1954). Young-of-the-year crabs are highly cannibalistic (Fernandez 1993).

Predators: Adults are commercially and recreationally harvested for food. In Washington and Oregon, *C. magister* is the most economically important fishery and the second most in California (Rasmuson 2013). Larval forms are eaten by plankton feeders (herring, salmon, other fishes). Juveniles and adults are commonly consumed by benthic fishes (Reilly 1983; Armstrong et al. 2003). *Cancer magister* equate to ~15% of the diet of sea otters in southeast Alaska. The egg broods of *C. magister* are predated by the nemertean worm, *Carcinonemertes errans* (Wickham 1979a, b) that can significantly reduce egg clutch size (Wickham 1986).

Behavior: Tagging studies report movement distances ranging from 0.2 to >100 km though the average is 1.1–3.2 km (Cleaver 1949; Hildenbrand et al. 2012). Juveniles and

adults are adept at digging both to bury within sediment and are also able to capture infaunal organisms (Butler 1954; Stevens et al. 1982).

Bibliography:

1. ANDERSON, W. 1978. A description of laboratory-reared larvae of the yellow crab, *Cancer anthonyi* Rathburn (Decapoda: Brachyura) and comparison with larvae of *Cancer magister* Dana and *Cancer productus* Randall. *Crustaceana*. 34:55-68.
2. ARMSTRONG, D. A., C. ROOPER, and D. GUNDERSON. 2003. Estuarine production of juvenile Dungeness crab (*Cancer magister*) and contribution to the Oregon-Washington coastal fishery. *Estuaries*. 26:1174-1188.
3. BUTLER, T. 1954. Food of the commercial crab in the Queen Charlotte Islands regions. Canadian Fisheries Research Board Pacific Progress Report. 99:3-5.
4. CLEAVER, F. C. 1949. Preliminary results of the coastal crab (*Cancer magister*) investigation. State of Washington, Dept. of Fisheries, [Olympia].
5. DUNN, P. H., and C. M. YOUNG. 2013. Finding refuge: The estuarine distribution of the nemertean egg predator *Carcinonemertes errans* on the Dungeness crab, *Cancer magister*. *Estuarine Coastal and Shelf Science*. 135:201-208.
6. —. 2014. Larval settlement of the nemertean egg predator *Carcinonemertes errans* on the Dungeness crab, *Metacarcinus magister*. *Invertebrate Biology*. 133:201-212.
7. FERNANDEZ, M., D. ARMSTRONG, and O. IRIBARNE. 1993. First cohort of young-of-the-year Dungeness crab, *Cancer magister*, reduces abundance of subsequent cohorts in intertidal shell habitat. *Canadian Journal of Fisheries and Aquatic Sciences*. 50:2100-2105.
8. FISHER, W. S., and D. E. WICKHAM. 1976. Mortalities and epibiotic fouling of eggs from wild populations of Dungeness crab, *Cancer magister*. *Fishery Bulletin*. 74:201-207.
9. GUTERMUTH, F. B., and D. A. ARMSTRONG. 1989. Temperature dependent metabolic response of juvenile Dungeness crab, *Cancer magister* Dana: ecological implications for estuarine and coastal populations. *Journal of Experimental Marine Biology and Ecology*. 126:135-144.
10. HARRISON, M. K., and B. J. CRESPI. 1999. Phylogenetics of Cancer crabs (Crustacea : Decapoda : Brachyura). *Molecular Phylogenetics and Evolution*. 12:186-199.
11. HILDENBRAND, K., R. EDER, and A. GLADICS. 2012. Adult male Dungeness crab (*Cancer magister*) movements near Reedsport, Oregon from a fisheries collaborative mark-recapture study. *Journal of Shellfish Research*. 31:296-297.
12. HUNTER, K. C., and P. P. RUDY. 1975. Osmotic and ionic regulation in Dungeness crab, *Cancer magister*. *Comparative Biochemistry and Physiology Part A*. 51:439-447.
13. JAFFE, L. A., C. F. NYBLADE, R. B. FORWARD, and S. SULKIN. 1987. Phylum or subphylum Crustacea, class Malacostraca, order Decapoda, Brachyura, p. 451-475. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
14. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
15. KURIS, A. M. 1993. Life cycles of nemerteans that are symbiotic egg predators of decapod crustacea: adaptations to host life histories. *Hydrobiologia*. 266:1-14.
16. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to*

- Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
17. MARTIN, J. W. 2014. Brachyura, p. 295-310. *In: Atlas of crustacean larvae*. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
 18. MCGAW, I. J. 2005. Burying behaviour of two sympatric crab species: *Cancer magister* and *Cancer productus*. *Scientia Marina*. 69:375-381.
 19. PAULEY, G. B., D. A. ARMSTRONG, R. VAN CITTER, and G. L. THOMAS. 1989. Species Profiles, Life histories and environmental requirements of coastal fishes and invertebrates. Pacific southwest: Dungeness crab.
 20. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 21. RASMUSON, L. K. 2013. The Biology, ecology and fishery of the Dungeness crab, *Cancer magister*. *Advances in Marine Biology*. 65:95-148.
 22. RASMUSON, L. K., and A. L. SHANKS. 2014. In situ observations of Dungeness crab megalopae used to estimate transport distances by internal waves. *Marine Ecology Progress Series*. 511:143-152.
 23. RATHBUN, M. J. 1930. The Cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. U.S. Government Printing Office, Washington, D.C.
 24. REILLY, P. N. 1983. Predation on Dungeness crabs, *Cancer magister*, in central California, USA. *Fish Bulletin*. 172:155-164.
 25. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 26. ROBINSON, G. D., and W. T. W. POTTS. 1979. Ion fluxes and diffusion potentials in the Dungeness crab, *Cancer magister*. *Journal of Comparative Physiology*. 131:285-292.
 27. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. *Invertebrate zoology: A functional evolutionary approach*. Thomson Brooks/Cole, Belmont, CA.
 28. SCHMITT, W. L. 1921. The marine decapod crustacea of California. University of California Publications in Zoology. 23:1-470.
 29. SCHRAM, F. R., and P. K. L. NG. 2012. What is Cancer? *Journal of Crustacean Biology*. 32:665-672.
 30. SCHWEITZER, C. E., and R. M. FELDMANN. 2000. Re-evaluation of the Cancridae Latreille, 1802 (Decapoda: Brachyura) including three new genera and three new species. *Contributions to Zoology*. 69:223-250.
 31. SHANKS, A. L. 2013. Atmospheric forcing drives recruitment variation in the Dungeness crab (*Cancer magister*), revisited. *Fisheries Oceanography*. 22:263-272.
 32. SNOW, C. D., and J. R. NIELSEN. 1966. Pre-mating and mating behavior of the Dungeness crab. *Journal of the Fisheries Research Board of Canada*. 23:1319-1323.
 33. STEVENS, B. G., D. A. ARMSTRONG, and R. CUSIMANO. 1982. Feeding habits of the Dungeness crab, *Cancer magister*, as determined by the index of relative importance. *Marine Biology*. 72:135-145.
 34. WALDRON, K. D. 1958. The fishery and biology of the Dungeness crab (*Cancer magister* Dana) in Oregon waters. Contribution, Oregon Fish Commission. 24:1-43.
 35. WEYMOUTH, F. W. 1914. Contributions to the life-history of the Pacific coast edible crab. Report of the British Columbia Commission of Fisheries. 1914:123-129.
 36. WICKHAM, D. E. 1979a. Predation by the nemertean *Carcinonemertes errans* on eggs of the Dungeness crab *Cancer magister*. *Marine Biology*. 55:45-53.
 37. —. 1979b. The Crab-egg predator, *Carcinonemertes errans*: a cycling and collapse of Dungeness Crab Population. Ph.D., University of California, Berkeley, CA.

38. —. 1986. Epizootic infestations by nemertean brood parasites on commercially important crustaceans. *Canadian Journal of Fisheries and Aquatic Sciences*. 43:2295-2302.
39. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.
40. WILD, P. W., and R. N. TASTO. 1983. Life history environment and

mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California USA fishery resource. *Fish Bulletin*. 172:1-352.

Updated 2015

T.C. Hiebert and L. Rasmuson

Cancer oregonensis

The Oregon *Cancer* crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Brachyura
Family: Cancridae

Taxonomy: Several synonyms are listed for the species *Cancer oregonensis* (e.g. *Platycarcinus recurvidens*, *Trichocarcinus walkeri*, *Trichocera oregonensis*), but the most recent taxonomic debate involves the placement of this species in the recently elevated genus, *Glebocarcinus* (Schweitzer and Feldmann 2000). Molecular work does not always support the monophyly of cancrid genera (Harrison and Crespi 1999) and although many researchers have switched to the name *Glebocarcinus oregonensis* (e.g. Wicksten 2011), we follow the most current local intertidal guide that retains the name *Cancer oregonensis* (Kuris et al. 2007).

Description

Size: Individuals are usually not over 40 mm wide (Kozloff 1993). Large females are 47.1 mm wide and 36.5 mm long (Rathbun 1930). The illustrated (Fig. 1) specimen is 15 mm wide and 11 mm long.

Color: Carapace reddish dorsally, sometimes red, orange or yellow pigment spots or bands, and flesh-colored ventrally. Walking legs (pereopods) with dark red to black cheliped tips and can have bands of light color or red spots. There is considerable variation in color from yellow to orange with carapaces that are sometimes gray (Jensen 1995; Wicksten 2011).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are reduced and folded ventrally (Decapoda, Kuris et al. 2007).

Cephalothorax:

Eyes: Eye stocks short.

Antennae: Antennules folded lengthwise (Fig. 3) bear short, hairy flagella.

Mouthparts: The mouth of decapod crustaceans is comprised of six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover it and the mandibles (Ruppert et al. 2004). The outer maxillipeds in *C. oregonensis* have with merus at antero-external angle (Fig. 2).

Carapace: Broadly oval, subelliptical (Rathbun 1930), widest at teeth 7–8 and aerolated. Anterior-lateral and posterior-lateral margins do not form a distinct angle (*C. oregonensis*, Rathbun 1930; Garth and Abbott 1980). Postero-lateral margin unbroken, entire and without teeth. Antero-lateral and postero-lateral margins meet without strong angle (Fig. 1). A characteristic that separates the (proposed) genus *Glebocarcinus* from other cancrid genera is a rounded carapace with length $\frac{3}{4}$ maximum width, as seen in *C. oregonensis* (Schweitzer and Feldmann 2000; Schram and Ng 2012).

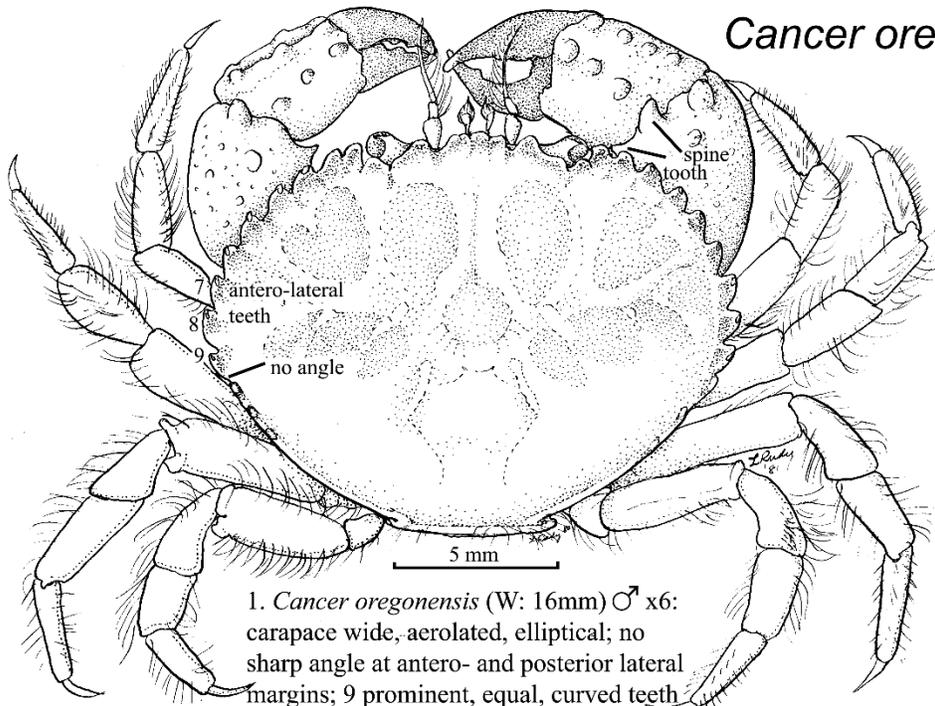
Frontal Area: Wide frontal area (about 1/2 width of carapace). Five truncate frontal teeth extend slightly beyond outer orbital angles. Three central teeth lobed (*C. oregonensis*, Rathbun 1930). Outer pair of teeth form inner orbital angles (Fig. 3).

Teeth: 12–13 antero-lateral teeth, of which the first nine are prominent, equal, large and forward curving. Teeth 3–9 have spines, teeth 10–13 are small, obscure or absent.

Pereopods: Walking legs hairy, light colored and with darkly pigmented dactyls.

Chelipeds: Dark nearly to tips (Fig. 4), carpus (wrist) tuberculate above, short spine at inner angle with tooth below. Hand (propodus) thick and high, with two rows of tubercles above and five granulate lines on outer surface (Fig. 4). Chelae rougher in females than in males (Rathbun 1930).

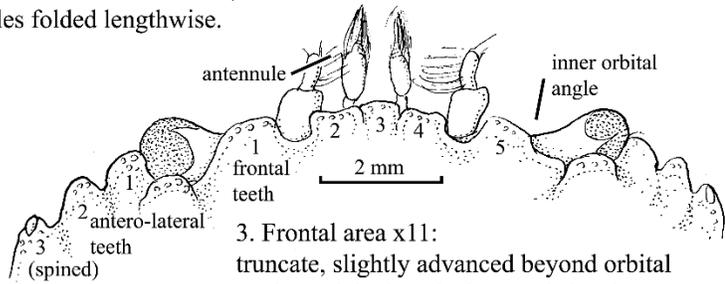
Cancer oregonensis



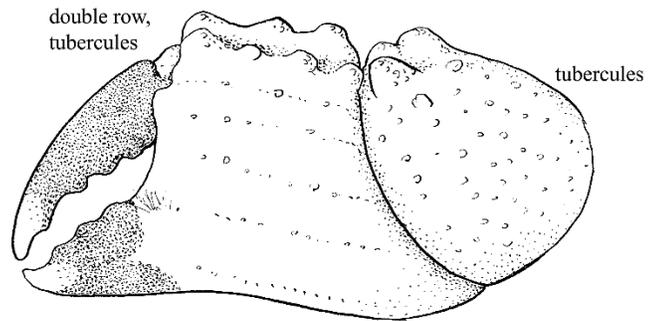
1. *Cancer oregonensis* (W: 16mm) ♂ x6:
 carapace wide, aerolated, elliptical; no sharp angle at antero- and posterior lateral margins; 9 prominent, equal, curved teeth (12-13 total); carapace widest at teeth 7-8; legs hairy; antennules folded lengthwise.



2. Maxilliped (ventral view) x11:
 produced at antero-external angle of merus.



3. Frontal area x11:
 truncate, slightly advanced beyond orbital angles; 5 lobed teeth: 3 central, 2 at inner orbital angles; eyestalks short; antero-lateral teeth 3-9 spined; antennules fold down.



4. Left cheliped x11 (outside):
 double row of tubercles, 5 rows fine granulate lines: hand; fingers dark almost to tips; wrist tuberculate.

Abdomen (Pleon): Abdomen narrow in male, broad in female (e.g. see *Cancer magister*, Fig. 3).

Telson & Uropods:

Sexual Dimorphism: Male and female brachyuran crabs are easily differentiable. The most conspicuous feature, the abdomen, is narrow and triangular in males while it is wide and flap-like in females. Additionally, males have one large chelae and two pleopod pairs specialized for copulation, however, the third and fourth pleopods are absent. Females, on the other hand, have all four pleopod pairs, each with long setae for egg attachment (Brachyura, Kuris et al. 2007). Female *C. oregonensis* often have a more uneven and lumpy textured carapace (sometimes with high, flattened elevations) and rougher chelae than males.

Possible Misidentifications

According to some authors, the genus *Cancer* comprises 23 species (Harrison and Crespi 1999 but see Schweitzer and Feldmann 2000). This genus is differentiated from other brachyuran genera by the broadly oval carapace, presence of five frontal teeth and antennules that fold back over carapace. Characters unique to *Cancer oregonensis* include 12–13 antero-lateral teeth, carapace widest at 7–8 tooth, red color, black-tipped cheliped dactyls and small size (Kuris et al. 2007). *Cancer oregonensis* is the only member of the genus with a distinctly elliptical carapace, without distinct angle at the posterior-anterior margin. It is smaller than most of the other adult *Cancer* species, but can be confused with their juveniles, which occur only seasonally, not all year, as will *C. oregonensis*. The key characteristic is the rounded, not angled carapace shape. *Cancer oregonensis* occupies a very particular niche: in the under-rock habitat, often found nestled in a well-fitting discarded mollusk or barnacle shell (Garth and Abbott 1980; Kozloff 1993).

There are eight *Cancer* species known locally (Kuris et al. 2007) and three of those are larger than *C. oregonensis* in their adult form including, *C. magister* (adults at least 30 mm in width), *C. productus* (adults over 20 mm in width) and *C. antennarius* (adults typically 100 mm in width). *Cancer productus* and *C. magister* have 10 antero-lateral teeth and five subequal frontal teeth (Kuris et al. 2007). The carapace of *C. magister* is widest at the tenth tooth, is more subtly pigmented

and does not have black tipped dactyls seen in *C. productus* (Wicksten 2011). The two species are often collected together in crab pots. *Cancer antennarius*, like *C. productus*, is dark red with spots ventrally and with black tipped chelae. However, the carapace width in *C. antennarius* is widest at the eighth tooth and there are a total of 11 antero-lateral teeth (Schmitt 1921; Kuris et al. 2007; Wicksten 2011).

The remaining four species tend to be smaller and have nine antero-lateral teeth (sometimes ten in older specimens, Wicksten 2011). *Cancer branneri* is a small species (35 mm) that is rare intertidally and recognizable by cheliped dactyls that are long, straight, black and spiny. *Cancer gracilis* (27 mm) has white-tipped cheliped dactyls and *C. jordani* (25 mm) has a hairy carapace and sharp curving teeth. *Cancer anthonyi*, the yellow rock crab, is larger than the previous three at 52 mm and has black-tipped cheliped dactyls (Kuris et al. 2007; Wicksten 2011). Populations of *C. productus*, *C. anthonyi* (southern California) and *C. magister* support commercial fisheries (Kuris et al. 2007).

Ecological Information

Range: Type locality is Puget Sound, Washington. Known range includes Aleutian Islands in Alaska to Lower California (Schmitt 1921; Ricketts and Calvin 1971; Wicksten 2011). Rare south of Oregon (Kuris et al. 2007).

Local Distribution: Coos Bay distribution at Fossil and Pigeon points.

Habitat: Rocky intertidal and subtidal areas of quiet bays, tidepools and well embedded rock and mud. Likes closely fitting shells, crannies.

Salinity: Found at lower (saltier) end of bays.

Temperature: A cold and temperate water dweller (by geographical range).

Tidal Level: Low intertidal to 435 m (Rathbun 1930; Wicksten 2011).

Associates: In the under-rock low intertidal of bays associates include burrowing clams (Pholadidae), terebellid polychaete *Thelepus* and its associate *Halosydna*. Subtidally, the large barnacle *Balanus nubilis*, whose discarded shell is often home to *C. oregonensis*. A parasitic barnacle (Rhizocephalan) becomes prevalent in Alaskan animals (Ricketts and Calvin 1971).

Abundance: Occurs commonly within its habitat.

Life-History Information

Reproduction: All decapod crustacean females attach recently laid gelatinous egg masses to their pleopods. The outer embryo membrane thickens and a strand develops that attaches each embryo to pleopod setae (Decapoda, Kuris et al. 2007). Mating occurs from April–June (Puget Sound, Washington), when the female is about to molt, male *C. oregonensis* clasp females several days prior to molting and copulation takes place after molting occurs. Fertilization is internal and occurs after molting and egg deposition occurs months later, November–March (December, Coos Bay) (Garth and Abbott 1980; Jaffe et al. 1987). Eggs are bright orange and approximately 400 µm in diameter and each brood contains approximately 20,500 eggs (Knudsen 1964). A second brood is sometimes produced after the first hatches (Jaffe et al. 1987). Eyespots and chromatophores are easily visible in advanced embryos (Jaffe et al. 1987; Kuris et al. 2007).

Larva: Larval development proceeds via a series of zoea (five total, telson with single lateral spine at each fork, Lough 1975) and megalopae stages, each marked by a molt. *Cancer oregonensis* zoea are planktotrophic and have large compound eyes and four spines: one each dorsal and rostral and two lateral (Lough 1975; see *Cancer* spp., Fig. 31, Puls 2001; Martin 2014). Larval size (measured from tip of rostrum to tip of telson) proceeds from 1.6 mm (Zoea I) to 2.3 mm (Zoea V) (Puls 2001). Megalopae are of similar size to *C. productus*, at 3.4 mm (from rostrum tip to posterior carapace) and total larval duration is unknown (Puls 2001). The zoea and megalopae of cancrid species are difficult to distinguish. The megalopae of *C. oregonensis* and *C. productus* were described by DeBrosse et al. 1990 (see Fig. 1-2, 3-4, DeBrosse et al. 1990).

Juvenile: Very much like adults (Schmitt 1921).

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the

ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: Predator and scavenger on other small invertebrates, especially barnacles (Jaffe et al. 1987).

Predators:

Behavior: Reclusive.

Bibliography

1. DEBROSSE, G. A., A. J. BALDINGER, and P. A. MCLAUGHLIN. 1990. A Comparative study of the megalopal stages of *Cancer oregonensis* Dana and *Cancer productus* Randall (Decapoda: Brachyura: Cancridae) for the northeastern Pacific. *Fishery Bulletin*. 88:39-49.
2. GARTH, J. S., and D. P. ABBOTT. 1980. Brachyura: the true crabs, p. 594-630. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
3. HARRISON, M. K., and B. J. CRESPI. 1999. Phylogenetics of Cancer crabs (Crustacea : Decapoda : Brachyura). *Molecular Phylogenetics and Evolution*. 12:186-199.
4. JAFFE, L. A., C. F. NYBLADE, R. B. FORWARD, and S. SULKIN. 1987. Phylum or subphylum Crustacea, class Malacostraca, order Decapoda, Brachyura, p. 451-475. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
5. JENSEN, G. C. 1995. Pacific coast crabs and shrimps. *Sea Challengers*, Monterey, CA.
6. KNUDSEN, J. W. 1964. Observations of the reproductive cycles and ecology of the common Brachyura and crablike Anomura of Puget Sound, Washington. *Pacific Science*. 18:3-33.
7. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.

8. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. T. Carlton (ed.). University of California Press, Berkeley, CA.
9. LOUGH, R. G. 1975. Dynamics of crab larvae (Anomura: Brachyura) off the central Oregon coast, 1969-1971. Ph.D. Oregon State University, Corvallis, OR.
10. MARTIN, J. W. 2014. Brachyura, p. 295-310. *In: Atlas of crustacean larvae.* J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
11. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine invertebrates of the Pacific Northwest.* A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
12. RATHBUN, M. J. 1930. The Cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. U.S. Government Printing Office, Washington, D.C.
13. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides.* Stanford University Press, Stanford, California.
14. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach.* Thomson Brooks/Cole, Belmont, CA.
15. SCHMITT, W. L. 1921. *The marine decapod crustacea of California.* University of California Publications in Zoology. 23:1-470.
16. SCHRAM, F. R., and P. K. L. NG. 2012. What is Cancer? *Journal of Crustacean Biology.* 32:665-672.
17. SCHWEITZER, C. E., and R. M. FELDMANN. 2000. Re-evaluation of the Cancridae Latreille, 1802 (Decapoda: Brachyura) including three new genera and three new species. *Contributions to Zoology.* 69:223-250.
18. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

T.C. Hiebert and A. Burgess

Cancer productus

The red rock crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda, Reptantia
Section: Brachyura
Family: Cancridae

Taxonomy: Despite recent confusion regarding a variety of cancrid genera, the taxonomy of *Cancer productus* has remained stably within the genus *Cancer* (Harrison and Crespi 1999; Schweitzer and Feldmann 2000; Kuris et al. 2007; Wicksten 2012).

Description

Size: Carapace 97–174 mm in length and up to 157.5 mm in width (Schmitt 1921; Rathbun 1930). Females with carapace length up to 158 mm and males up to 200 mm (Puls 2001).

Color: Dark red dorsally, lighter ventrally, legs mottled red and juveniles striped (Fig. 3).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are reduced and folded ventrally (Decapoda, Kuris et al. 2007).

Cephalothorax:

Eyes: Eystalks short, orbits small.

Antennae: Antennules folded lengthwise, antennal flagella short and hairy (Queen 1930).

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004).

Carapace: Broadly oval, uneven and slightly convex. Widest at ninth antero-lateral tooth (Fig. 1) (Wicksten 2012).

Frontal Area: Markedly pronounced beyond eyes, with five nearly equal teeth (Fig. 2).

Teeth: Ten antero-lateral teeth (counting orbital tooth), nine large teeth that become more acute posteriorly.

Pereopods: Dactyls thickly fringed above and below.

Chelipeds: Dactyls dark-tipped and hands rough dorsally. Carpus wrinkled, with single tooth at inner angle (Queen 1930).

Abdomen (Pleon): Abdomen narrow in male, broad in female (e.g. see *Cancer magister*, Fig. 3).

Telson & Uropods:

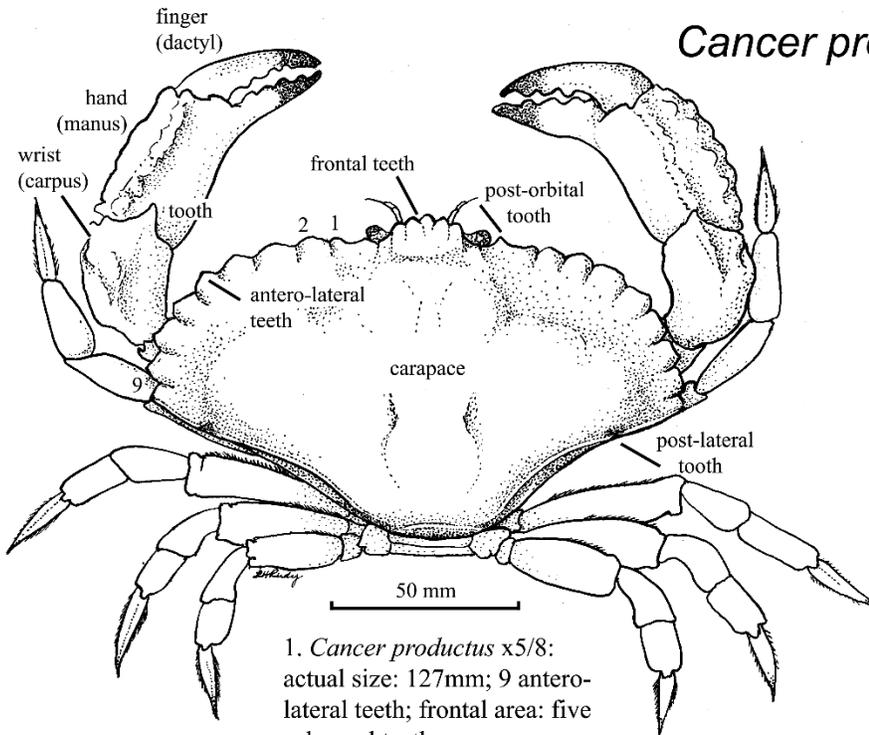
Sexual Dimorphism: Male and female brachyuran crabs are easily differentiable. The most conspicuous feature, the abdomen, is narrow and triangular in males while it is wide and flap-like in females. Additionally, males have one large chelae and two pleopod pairs specialized for copulation however, the third and fourth pleopods are absent. Females, on the other hand, have all four pleopod pairs, each with long setae for egg attachment (Brachyura, Kuris et al. 2007).

Possible Misidentifications

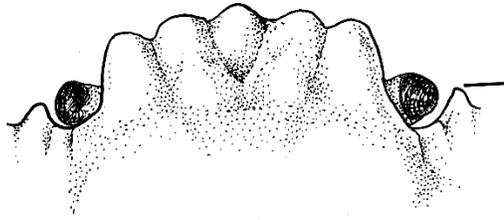
According to some authors, the genus *Cancer* comprises 23 species (Harrison and Crespi 1999 but see Schweitzer and Feldmann 2000). This genus is differentiated from other brachyuran genera by the broadly oval carapace, presence of five frontal teeth and antennules that fold back over carapace. Characters unique to *Cancer productus* include ten antero-lateral teeth, carapace widest at ninth tooth, bright red color and black-tipped cheliped dactyls (Kuris et al. 2007).

There are eight *Cancer* species known locally (Kuris et al. 2007). The most morphologically similar to *C. productus* is *C. magister*, which also has 10 antero-lateral teeth and five subequal frontal teeth (Kuris et al. 2007). However, the carapace of *C. magister* is widest at the tenth tooth, is more subtly pigmented and does not have black tipped dactyls (Wicksten 2012). The two species are often collected together in crab pots. *Cancer antennarius*, like *C. productus*, is dark red with spots ventrally and with black tipped chelae. However the carapace width in *C. antennarius* is widest at the eighth tooth

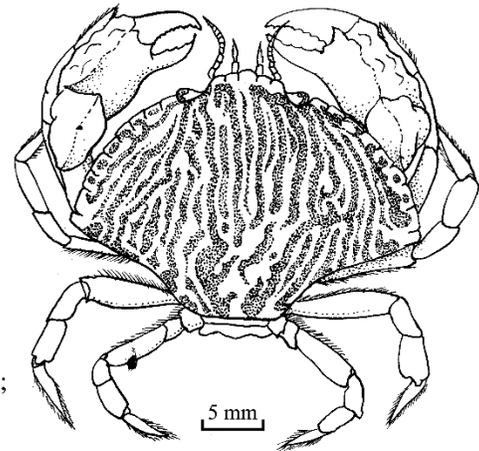
Cancer productus



1. *Cancer productus* x5/8:
actual size: 127mm; 9 antero-lateral teeth; frontal area: five subequal teeth; carapace broadly oval; fingers dark-tipped; one post-lateral tooth, one post-orbital tooth.



2. Frontal area: markedly pronounced; five subequal teeth; post-orbital tooth.



3. Juvenile x2:
actual size 2.5mm
carapace like adult; striped; nine antero-lateral teeth.

and there are a total of 11 antero-lateral teeth (Wicksten 2012). *Cancer oregonensis* is a small, oval crab with 12–13 total teeth. The remaining four species have nine antero-lateral teeth (sometimes ten in older specimens, Wicksten 2012). *Cancer branneri* is a small species (35 mm) that is rare intertidally and recognizable by cheliped dactyls that are long, straight, black and spiny. *Cancer gracilis* is also small (27 mm) has white-tipped cheliped dactyls and *C. jordani* (25 mm) has a hairy carapace and sharp curving teeth. *Cancer anthonyi*, the yellow rock crab, is larger than the previous three at 52 mm and has black-tipped cheliped dactyls (Kuris et al. 2007; Wicksten 2012). Populations of *C. productus*, *C. anthonyi* (southern California) and *C. magister* support commercial fisheries (Kuris et al. 2007).

Ecological Information

Range: Kodiak, Alaska, to Magdalena Bay, Baja California (Schmitt 1921).

Local Distribution: Occurs in a variety of local Oregon estuaries including Coos, Yaquina, Umpqua, Coquille, Tillamook (Gaumer et al 1973) on semi-protected rocky shores (Garth and Abbott 1980).

Habitat: Individuals appear to prefer gravel, rock, and hard bottom – *C. productus* does not burrow and lacks straining apparatus for sand removal (Ricketts and Calvin 1971). Also found in rocky tidepools and among eelgrass (Ricketts and Calvin 1971; Garth and Abbott 1980). Adults tend to bury themselves into soft sand as is seen in *C. magister*, although less frequently (McGaw 2004).

Salinity: Collected at 30. In San Francisco Bay salinity tolerance ranges from 21.7 to 33.3 (Schmitt 1921).

Temperature: Collected at 11–17°C in the San Francisco Bay area (Schmitt 1921).

Tidal Level: Intertidal to about 79 m and occurs closer to shore than *C. magister* (Puls 2001).

Associates:

Abundance: Common (Carlton and Kuris 1975).

Life-History Information

Reproduction: In *C. productus*, mating occurs June–August (Puget Sound) (Knudsen 1964; Jaffe et al. 1987). When the female is about to molt, male *C. productus* clasps the

female and copulation takes place after molting (i.e. female shell is soft). Fertilization is internal and egg deposition occurs months later in December–January, at which point eggs are bright orange. All decapod crustacean females attach recently laid gelatinous egg masses to their pleopods. The outer embryo membrane thickens and a strand develops that attaches each embryo to pleopod setae (Decapoda, Kuris et al. 2007). Eyespots and chromatophores are easily visible in advanced embryos and make them appear gray when ready to hatch. Zoea larvae hatch by early April (Knudsen 1964). A second brood is sometimes produced (Jaffe et al. 1987).

Larva: The larvae of *C. productus* have been described (Trask 1970; Roesijadi 1976). Larval development proceeds via a prezoaea (Roesijadi 1976) followed by a series of zoea (five total, telson with single lateral spine at each fork, Lough 1975) and megalopae stages, each marked by a molt. The zoea and megalopae of cancrinid species are difficult to distinguish. The larvae of *C. productus*, *C. oregonensis* and *C. magister* are morphologically similar (Puls 2001), but can be differentiated (e.g. variation in setal morphology, see Trask 1970). *Cancer productus* zoea are planktotrophic and have large compound eyes and four spines: one each dorsal and rostral and two lateral (see Fig. 1, Trask 1970; Martin 2014), which are lacking in prezoaeae (Roesijadi 1976). Larval size (measured from tip of rostrum to tip of telson) proceeds from 2.5 mm (Zoea I and telson with pair of lateral exospines) to approximately 6 mm (Zoea V) (Trask 1970; Puls 2001). The megalopae of *C. productus* are about half the size of *C. magister* megalopae (3.4–3.6 mm from rostrum to posterior carapace and approximately 2 mm at widest point) (Trask 1970). Larvae have been observed swarming in May (Friday Harbor, Jaffe et al. 1987). Hatching zoea to the megalopa stage requires 97 days in the lab (Trask 1970). The megalopae of *C. oregonensis* and *C. productus* were described by DeBrosse et al. 1989 (see Fig. 1-2, 3-4, DeBrosse et al. 1989).

Juvenile: Juveniles are often brightly colored and possess several to many spots (see Krause-Nehring et al. 2010). Interestingly, the wide variety of juvenile color morphs does not correspond to environmental background

colors or food (Krause-Nehring et al. 2010). The carapace is widest at ninth tooth, naked and often spotted or striped. Frontal and antero-lateral teeth are flat, rounded and fairly uniform (Fig. 3).

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007). Research has shown, however, that regenerated limbs handicap *C. productus* foraging and predatory abilities (Brock and Smith 1998).

Food: *Cancer productus* individuals are scavengers and predators on other crustaceans, especially barnacles and other crabs (Knudsen 1964) as well as molluscs and polychaete worms. Zoea reportedly ingest *Dendraster excentricus* pluteus larvae, but their efficiency reduces with pluteus size and age (Rumrill et al. 1985).

Predators: Adults are commercially and recreationally harvested for food. Additional predators include octopus, fish and birds (Knudsen 1964). Larval forms are predated by filter and plankton feeders (herring, salmon, and other fishes).

Behavior: Individuals are dominant and stalk prey in tidepools at night (Ricketts and Calvin 1971). They are also active in daylight and individuals can aggregate by sex and age, depending on egg-laying and molting cycles (Knudsen 1964).

Bibliography

1. BROCK, R. E., and L. D. SMITH. 1998. Recovery of claw size and function following autotomy in *Cancer productus* (Decapoda: Brachyura). *Biological Bulletin*. 194:53-62.
2. DEBROSSE, G. A., A. J. BALDINGER, and P. A. MCLAUGHLIN. 1990. A Comparative study of the megalopal stages of *Cancer oregonensis* Dana and *Cancer productus* Randall (Decapoda: Brachyura: Cancridae) for the

- northeastern Pacific. *Fishery Bulletin*. 88:39-49.
3. GARTH, J. S., and D. P. ABBOTT. 1980. Brachyura: The true crabs, p. 594-630. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
4. GAUMER, T., and E. AL. 1973. Estuary resource use studies. Oregon Fish Commission, Portland, OR.
5. HARRISON, M. K., and B. J. CRESPI. 1999. Phylogenetics of cancer crabs (Crustacea: Decapoda: Brachyura). *Molecular Phylogenetics and Evolution*. 12:186-199.
6. KNUDSEN, J. W. 1964. Observations of the reproductive cycles and ecology of the common Brachyura and crablike Anomura of Puget Sound, Washington. *Pacific Science*. 18:3-33.
7. KRAUSE-NEHRING, J., J. M. STARCK, and A. R. PALMER. 2010. Juvenile colour polymorphism in the red rock crab, *Cancer productus*: patterns, causes, and possible adaptive significance. *Zoology*. 113:131-139.
8. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
9. LOUGH, R. G. 1975. Dynamics of crab larvae (Anomura: Brachyura) off the central Oregon coast, 1969-1971. Ph.D. Oregon State University, Corvallis, OR.
10. MARTIN, J. W. 2014. Brachyura, p. 295-310. *In: Atlas of crustacean larvae*. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
11. MCGAW, L. J. 2004. Ventilatory and cardiovascular modulation associated with burying behaviour in two sympatric crab species, *Cancer magister* and *Cancer productus*. *Journal of Experimental Marine Biology and Ecology*. 303:47-63.
12. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine*

- invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
13. QUEEN, J. C. 1930. Marine decapod crustacea of the Coos Bay, Oregon District. M.S. University of Oregon, Eugene, OR.
 14. RATHBUN, M. J. 1930. The Cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. U.S. Government Printing Office, Washington, D.C.
 15. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 16. ROESIADI, G. 1976. Descriptions of the prezoae of *Cancer magister* Dana and *Cancer productus* Randall and the larval stages of *Cancer antennarius* Stimpson (Decapoda: Brachyura). *Crustaceana*. 31:275-295.
 17. RUMRILL, S. S., J. L. PENNINGTON, and F. S. CHIA. 1985. Differential susceptibility of marine invertebrate larvae: laboratory predation of sand dollar, *Dendraster excentricus* (Eschscholtz) embryos and larvae by zoeae of the red crab, *Cancer productus* Randall. *Journal of Experimental Biology*. 90:193-208.
 18. SCHMITT, W. L. 1921. The marine decapod crustacea of California. University of California Publications in Zoology. 23:1-470.
 19. SCHWEITZER, C. E., and R. M. FELDMANN. 2000. Re-evaluation of the Cancridae Latreille, 1802 (Decapoda: Brachyura) including three new genera and three new species. *Contributions to Zoology*. 69:223-250.
 20. TRASK, T. 1970. A Description of laboratory reared larvae of *Cancer productus* (Decapoda: Brachyura) and a comparison to the larvae of *Cancer magister*. *Crustaceana*. 18:133-146.
 21. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

Pugettia producta

A kelp crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Brachyura
Family: Epialtidae

Taxonomy: *Pugettia producta* was originally described as *Epialtus productus* by Randall in 1840, but was later moved to the genus *Pugettia*. Current synonyms for *P. producta* include *E. products*, and *P. productus* (Ng et al. 2008).

Description

Size: *Pugettia producta* is the largest of the kelp crabs (Wicksten 2011) and the largest individual, on record, was 93 mm in width and 107 mm in length. Oregon specimens are larger than those in southern California. The average male carapace is 71 mm in length and 62 mm in width, female carapace is 69 mm in length and 59 mm in width (Wicksten 2011).

Color: Body color highly dependent on season, molting stage and ingested macroalgal pigments (Hultgren and Stachowicz 2008) and ranges from light olive green to dark brown or black. Ventrally, females and juveniles are often yellow and males bright red (see Wicksten 2011).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are reduced and folded ventrally (Decapoda, Kuris et al. 2007).

Cephalothorax:

Eyes: Eyes small and distance between them less than one third carapace width (adults).

Antennae:

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004).

Carapace: Carapace remarkably smooth and mature specimens are practically hairless (Garth 1958). Sides of carapace are almost parallel with prominent posterolateral teeth (*Pugettia*, Carlton and Kuris 1975). Posterior margin convex medially (Garth 1958) and carapace decidedly longer than wide (Wicksten 2011).

Frontal Area: Rostrum deeply notched and bifid, small and with horns bearing hooked setae (Garth 1958; Wicksten 2011) (Figs. 1, 2).

Teeth: Dorsal surface smooth with small pre- and post-orbital teeth (Fig. 2). Large anterolateral (hepatic) teeth. Large hepatic tooth is joined to postorbital tooth. A large tooth is also present between anterolateral tooth and posterior margin.

Pereopods: Almost cylindrical (Rathbun 1925) and decreasing in length posteriorly with slender dactyls that bear spinules (Fig. 1) (Garth 1958; Wicksten 2011). Legs shorter and stouter than in other *Pugettia* species.

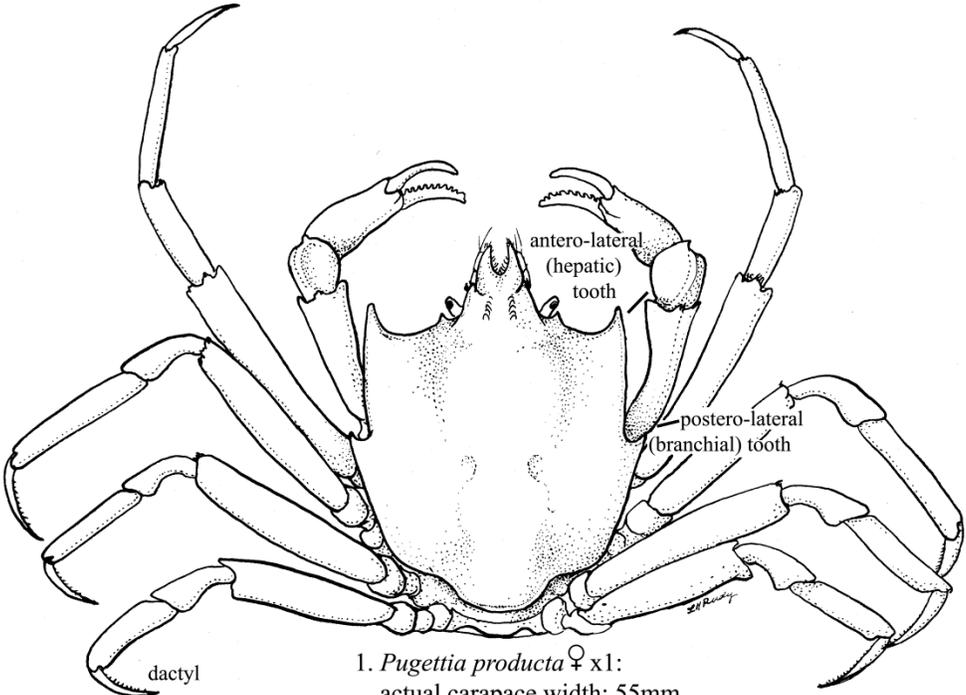
Chelipeds: Large and well developed, especially in mature males, where they are stout and shorter than the first walking legs. The hand long and narrow (sometimes inflated), fingers (dactyls) are slender, pointed posteriorly and curved inward, inner margins are dentate and often gaping (males). Female chelipeds, on the other hand, are slender (Fig. 3) (Rathbun 1925). Female cheliped more slender than male (Wicksten 2011).

Abdomen (Pleon): Abdomen narrow in male, broad in female (Fig. 4). Consists of seven segments (Fig. 4).

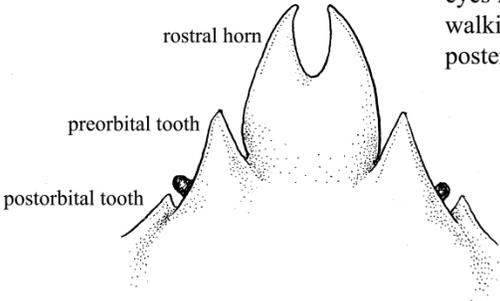
Telson & Uropods:

Sexual Dimorphism: Male and female brachyuran crabs are easily differentiable. The most conspicuous feature, the abdomen, is narrow and triangular in males while it is wide and flap-like in females. Additionally, males have one large chela (see **Chelipeds**) and two pleopod pairs specialized for copulation however, the third and fourth pleopods are absent. Females, on the other

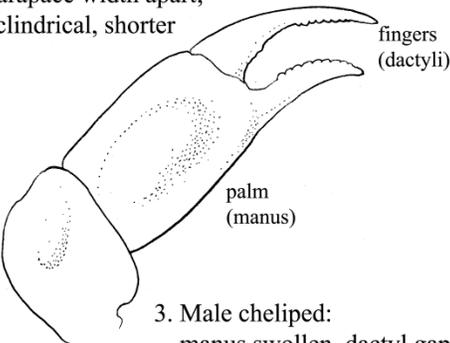
Pugettia producta



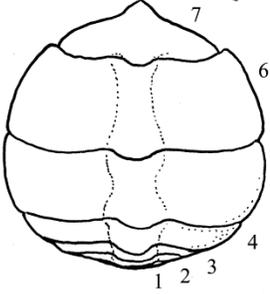
1. *Pugettia producta* ♀ x1:
 actual carapace width: 55mm
 carapace smooth, sides subparallel;
 strong hepatic and branchial teeth;
 eyes less than 1/3 carapace width apart;
 walking legs subcylindrical, shorter
 posteriorly.



2. Frontal area:
 rostrum bifid: two horns;
 small pre- and post- orbital
 teeth.



3. Male cheliped:
 manus swollen, dactyl gaping;
 often long, stout.



4. Abdomen ♀ (ventral view):
 seven segments.

(1&2 dorsal)

hand, have all four pleopod pairs, each with long setae for egg attachment (Brachyura, Kuris et al. 2007).

Possible Misidentifications

Among the Epialtidae, there are four local species, three of which belong to the genus *Pugettia* (Kuris et al. 2007). Besides *P. producta*, *Pugettia gracilis* and *Pugettia richii* are two smaller species found in the northwest. Both are smaller and have a greater distance between the eyes (about half the carapace width) than *P. producta*. Additionally, both have tuberculate carapace surfaces, constrictions between the hepatic and branchial teeth and long walking legs (Garth 1958, Wicksten 2011). Neither *P. gracilis* nor *P. richii* have the smooth surface or straight carapace sides of *P. producta*. *Pugettia gracilis* can be similar in color to *P. producta*, but *P. richii* is usually red with legs banded (Wicksten 2011). Members of the local epialtid genus *Mimulus* lack posterolateral spines.

Ecological Information

Range: Type locality is northern California. Known range includes Prince of Wales Island, Alaska to Point Asuncion, Baja California (Garth 1958; Wicksten 2011).

Local Distribution: Coos Bay distribution in South Slough. Oregon distribution includes various protected outer shores and estuaries.

Habitat: Off hard substrate and amongst eelgrass and kelp (*Egregia*, Ricketts and Calvin 1971). Also occurs in tidepools on *Fucus*, on pilings in bays and in *Enteromorpha*, but prefers *Zostera* (juveniles) (Garth and Abbott 1980).

Salinity: Collected at salinities of 30. Does not osmoregulate or tolerate brackish water (Garth and Abbott 1980).

Temperature:

Tidal Level: Intertidal to 80 meters (Garth 1958; Wicksten 2011).

Associates: Sometimes hosts parasitic barnacle, *Sacculina*. Eggs parasitized by nemertean worm *Carcinonemertes epialti* (Garth and Abbott 1980; Coe 1902; Kuris et al. 2007).

Abundance: Most common kelp crab in Coos Bay estuary.

Life-History Information

Reproduction: All decapod crustacean females attach recently laid gelatinous egg masses to their pleopods. The outer embryo membrane thickens and a strand develops that attaches each embryo to pleopod setae (Decapoda, Kuris et al. 2007). Ovigerous females have been observed year-round in Monterey Bay, California, although rarely during some months. In Puget Sound, Washington largest broods are observed in November to January. Brood numbers range from 34,000 to 84,000 with an average of 61,000 embryos that are yellow early in development and become orange-red to brown at more advanced stages (Jaffe et al. 1987). Developmental timelines are variable with latitude from 28–31 days in Monterey, California to almost a year in Puget Sound, Washington (Knudsen 1964; Jaffe et al. 1987). Females produce broods regularly and some authors suggest as often as monthly (Hines 1981; Jaffe et al. 1987). *Carcinonemertes epialti* is a nemertean predator of *P. producta* eggs (Coe 1902). Up to 100 nemerteans were found on a single crab (Monterey, California, Coe 1902). The reproduction and life-cycle of *C. epialti* is dependent upon and corresponds to that of its host species. However, this nemertean is not host specific (unlike *Carcinonemertes errans* on *Cancer magister*) and occurs amongst egg masses of other species including *Hemigrapsus oregonensis*, *H. nudus*, *Pachygrapsus crassipes* (Roe et al. 2007). Interestingly, it may be more common on *H. oregonensis* than *P. producta*, for which it was described (Kuris 1993; Kuris et al. 2007).

Larva: The larval development of *P. producta* has not been described in detail. Development consists of zoea (two) and megalopa stages (Hines 1981). The zoea of members of the family Majidae (now Epialtidae) can be recognized by the presence of a rostral spine only, lack of lateral spines and an antenna protopod that is nearly equal in length to the rostrum. The carapace of megalopae are 1.6 mm in length and 1.2 mm in width and is larger than its congener, *P. gracilis* (Puls 2001). Recruitment of newly metamorphosed individuals is mostly in intertidal and shallow subtidal eelgrass and surfgrass zones (Jaffe et al. 1987).

Juvenile: Juveniles (about 3 mm long) can be constricted at the sides like *P. richii* (Garth

1958). Newly settled individuals bear tufts of setae on the lateral margins of the carapace and are yellow in color, ventrally (Wicksten 2011).

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: *Pugettia producta* is primarily herbivorous, preferring brown algae, but will eat barnacles, mussels and fish pieces in the laboratory (Knudsen 1964). Ontogenetic changes from red intertidal algae to brown algae (kelp) has been reported by Hines (1982).

Predators: Fishes (especially juveniles), larger crabs and sea otters (Grossman 1986; Hultgren and Stachowicz 2008). Adult *P. producta* are aggressive with a strong pinch and thus, few predators. Additionally, color camouflage effective in reducing predation (Hultgren and Stachowicz 2008).

Behavior: A nocturnal feeder, *P. producta* is an active species, particularly those in rocky tide pools (Rathbun 1925). Individuals occasionally attach pieces of algae, which will be consumed later, to their rostrum (Wicksten 2011).

Bibliography

1. CARLTON, J. T., and A. M. KURIS. 1975. Keys to decapod crustacea, p. 385-412. *In*: Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
2. COE, W. R. 1902. The nemertean parasites of crabs. *American Naturalist*:431-450.
3. GARTH, J. S. 1958. Brachyura of the Pacific coast of America: Oxyrhyncha. Allan Hancock Pacific Expedition. 21:188-193.
4. GARTH, J. S., and D. P. ABBOTT. 1980. Brachyura: The true crabs, p. 594-630. *In*: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
5. GROSSMAN, G. D. 1986. Food resource partitioning in a rocky intertidal fish assemblage. *Journal of Zoology Series B*. 1:317-356.
6. HINES, A. H. 1981. Life history strategies of spider crab (Majidae). *American Zoologist*. 21:990-990.
7. —. 1982. Coexistence in a kelp forest: size, population dynamics, and resource partitioning in a guild of spider crabs (Brachyura: Majidae). *Ecological Monographs*. 52:179-198.
8. HULTGREN, K. M., and J. J. STACHOWICZ. 2008. Alternative camouflage strategies mediate predation risk among closely related co-occurring kelp crabs. *Oecologia*. 155:519-528.
9. JAFFE, L. A., C. F. NYBLADE, R. B. FORWARD, and S. SULKIN. 1987. Phylum or subphylum Crustacea, class Malacostraca, order Decapoda, Brachyura, p. 451-475. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
10. KNUDSEN, J. W. 1964. Observations of the reproductive cycles and ecology of the common Brachyura and crablike Anomura of Puget Sound, Washington. *Pacific Science*. 18:3-33.
11. KURIS, A. M. 1993. Life cycles of nemerteans that are symbiotic egg predators of decapod crustacea: adaptations to host life histories. *Hydrobiologia*. 266:1-14.
12. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
13. NG, P. K. L., D. GUINOT, and P. J. F. DAVIE. 2008. Systema brachyurorum: Part I. Annotated checklist of the extant Brachyuran crabs of the world. *Raffles Bulletin of Zoology Supplement*. 17:1-286.

14. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
15. RATHBUN, M. J. 1925. The Spider crabs of America. Bulletin of the United States Natural Museum. 129:167-172.
16. RICKETTS, E. F., and J. CALVIN. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
17. ROE, P., J. L. NORENBURG, and S. MASLAKOVA. 2007. Nemertea, p. 221-233. *In*: Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
18. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. Invertebrate zoology: a functional evolutionary approach. Thomson Brooks/Cole, Belmont, CA.
19. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

T.C. Hiebert and A. Burgess

Pachygrapsus crassipes

The lined shore crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Brachyura
Family: Grapsidae

Taxonomy: Until recently the brachyuran family Grapsidae, the shore crabs, was very large with several subfamilies and little taxonomic scrutiny. Based on molecular and morphological evidence, authors (von Sternberg and Cumberlidge 2000; Schubart et al. 2000; de Grave et al. 2009; Schubart 2011) elevated all grapsid subfamilies to the family level, reducing the number of species formally within the Grapsidae. Although recent molecular evidence suggest that *Hemigrapsus* is no longer within this family, *Pachygrapsus* remains one of the few members of the Grapsidae *sensu stricto* based on morphological evidence from adults, larvae and molecular data (Schubart 2011).

Description

Size: Carapace approximately 40 mm in width and males are larger than females (Hiatt 1948) (Fig. 1). Mature individuals weighed 15 g. (Gross and Marshall 1960) and measure 48 mm in width (Puls 2001).

Color: Dark green carapace, with dark red or blue transverse lines and some light markings (Plate 21, Kozloff 1993). Chela white ventrally and bright red dorsally (males) (Wicksten 2011).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are reduced and folded ventrally (Decapoda, Kuris et al. 2007).

Cephalothorax:

Eyes: Eyes present at anterolateral angle and eyestalks of moderate size with orbits deep and oblique (Fig. 2).

Antennae:

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The

maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004). The third maxilliped in *P. crassipes* has merus, lobate and at an angle (Wicksten 2011).

Carapace: Nearly square in shape and a little broader than long, transverse lines or grooves on anterior. Lateral margins are most broad posterior to orbit (Wicksten 2011). Carapace sides nearly parallel, but arched (Fig. 1).

Frontal Area: Broad margin that is smooth, slightly arched and half as wide as carapace. Four slight lobes present below margin with small lobes at outer corners (Fig. 2).

Teeth: One strong lateral carapace tooth (below the orbital tooth) (Fig. 2).

Pereopods: Merus of each leg broad and bearing a single tooth at each postero-distal angle, except the fifth (last) pair smooth at distal end, and no sharply distinct teeth (Fig. 3) (Wicksten 2011). Leg shape broad, compressed and bristled (Rathbun 1918). Dactyls spinulose (Wicksten 2011).

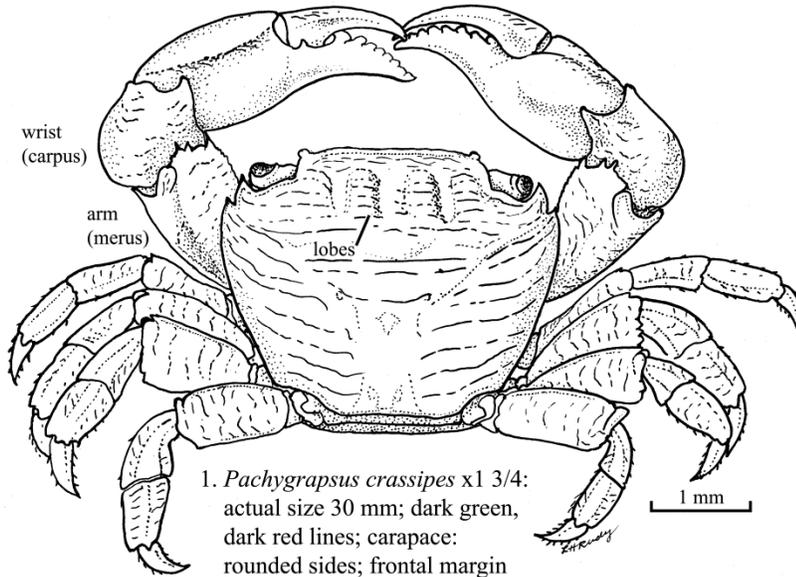
Chelipeds: Usually subequal and massive. Chela almost smooth with arm and wrist striated (Rathbun 1918). Male chela broad with raised line present on propodus, fingers spooned. Female chela, on the other hand, less broad.

Abdomen (Pleon): Females with wide abdomen and male *H. oregonensis* have narrow abdomens that exposes the sternum at the base (see **Sexual Dimorphism**, see Fig. 3, *Hemigrapsus oregonensis*).

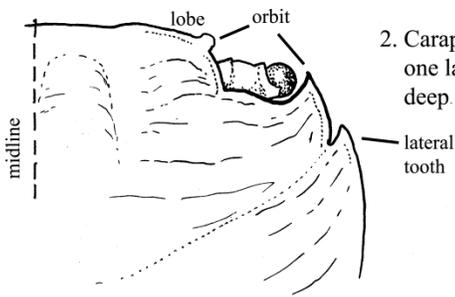
Telson & Uropods:

Sexual Dimorphism: Male and female brachyuran crabs are easily differentiable. The most conspicuous feature, the abdomen, is narrow and triangular in males while it is wide and flap-like in females (Brachyura, Kuris et al. 2007). Male *P. crassipes* abdomen is narrow and triangular, exposing sternum at sides (as in *Hemigrapsus nudus* and *H. oregonensis*.) Female abdomen is rounded, wide and hiding sternum in the

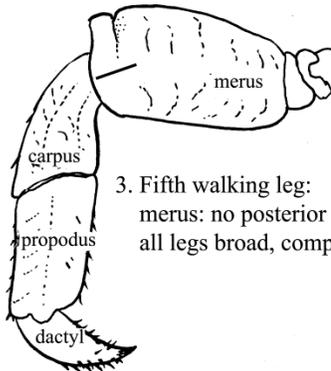
Pachygrapsus crassipes



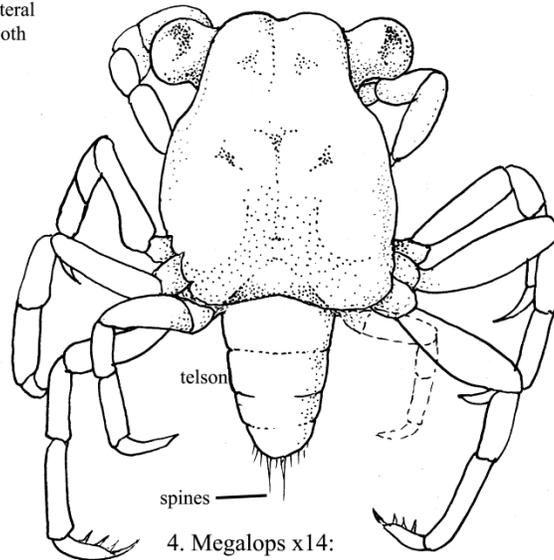
1. *Pachygrapsus crassipes* x1 3/4:
actual size 30 mm; dark green,
dark red lines; carapace:
rounded sides; frontal margin
straight; wrist and arm striated; four
lobes below frontal margin.



2. Carapace (right front):
one lateral tooth, one post-orbital;
deep orbits.



3. Fifth walking leg:
merus: no posterior teeth
all legs broad, compressed.



4. Megalops x14:
telson: two long spines
(from Hiatt, 1948).

adult. Dimorphism obvious when animals only 6 mm wide (Hiatt 1948).

Possible Misidentifications

Pachygrapsus species are members of the Grapsidae, a family characterized by the carpus of the third maxilliped not articulating near the anterior merus angle and by lateral mouth margins that are parallel or convergent (Wicksten 2011). There is only one local *Pachygrapsus* species, but it may be confused with other grapsid crabs from the family Varunidae, characterized by chelae morphology, gaping third maxillipeds and setose walking legs (Ng et al. 2008). *Pachygrapsus crassipes* is superficially similar to the slower *Hemigrapsus nudus*, but the latter has obvious red spots on its chelipeds, and lacks the dark green color and transverse striations of *P. crassipes*. Furthermore, the frontal margin of *P. crassipes* is straight and it has one lateral tooth, not two (Symons 1964). Two similar shore crabs in the genus *Hemigrapsus* are *H. oregonensis*, which is smaller, and *H. nudus*, with two lateral teeth and a smooth, square carapace. The only other species of *Pachygrapsus*, the smaller *P. transversus*, occurs only as far north as California. The only other locally occurring member of the Grapsidae, *Planes cyaneus*, is a pelagic species that is only found washed ashore on drift logs with gooseneck barnacles (Kuris et al. 2007). *Rhithropanopeus harrisi*, an introduced xanthid (Panopeidae) mud crab, occurs locally with shore crabs. It has a slightly convergent sides, strong dorsal ridges on its carapace and three sharp carapace teeth.

Ecological Information

Range: Type locality is probably Oregon (erroneously Hawaii, Hiatt 1948; Wicksten 2011). Known range includes Oregon to Gulf of California, however there is significant genetic structuring between populations north and south of Pt. Conception, California (Cassone and Boulding 2006).

Local Distribution: Northernmost boundary is 45° N (Newport, Oregon), probably due to cold winter temperatures found on protected rocky beaches and in southern Oregon estuaries.

Habitat: Prefers hard substrates, especially rocks, jetties and boulders with crevices and

crannies covered in algal growth. Also occurs in *Salicornia* marshes where *Salicornia* roots provide burrows.

Salinity: Most aspects of the biology of *P. crassipes*, in the following categories, were described by Hiatt (1948). Osmoregulatory adaptations indicate movement toward terrestrial habitat and can regulate against salt concentrations in the body during periods of exposure, and thus maintain a constant body salinity (Jones 1941). Occurs less frequently in brackish water than does *Hemigrapsus* (Hiatt 1948).

Temperature: Northern limit of range apparently determined by low winter temperatures and individuals can tolerate greater temperature fluctuation than can *Hemigrapsus* (Hiatt 1948).

Tidal Level: Lives over an extensive vertical range from mean low water to + 2.5 m. *Pachygrapsus crassipes* is found highest in intertidal of all Pacific Northwest crabs and is especially abundant at the higher levels (upper intertidal, Schmitt 1921) progressing toward terrestrial habitat (Hiatt 1948). However, as blood concentrations of potassium, calcium, and magnesium increase more than sodium when animal is desiccated, terrestrial adaptation may be inhibited. Also, efficiency of the animal's vascular system, affected by osmotic stress, further limits ecological range (Gross 1959).

Associates: *Pachygrapsus crassipes* occurs with *Hemigrapsus oregonensis* in bays, and with *H. nudus* on rocky outer shores. It competes with both for shelter (Hiatt 1948), but not for food. *Fucus* (alga) and *Salicornia* (pickleweed) often provide protection. Individuals can be infested by bopyrid isopods (Southern California, Schmitt 1921).

Hemigrapsus oregonensis, *H. nudus* and *P. crassipes* can be all be host to the nemertean egg predator, *Carcinonemertes epialti*, which can negatively impact brood mortality in these species (Shields and Kuris 1988). These three species can also serve as intermediate hosts for a variety of parasites including trematode metacercariae, trypanorhynch tapeworm, *Polymorphus acanthocephalan* and *Ascarophis* nematode larvae (Kuris et al. 2007).

Abundance: Ubiquitous in upper intertidal of rocky areas (Kuris et al. 2007) and more abundant on outer shores than in bays.

Life-History Information

Reproduction: No pairing or exhibitionism. Copulation occurs when females are soft (post-molting) and copulatory behavior has been described by Hiatt (1948) and Bovbjerg (1960a). Females ovigerous from April to September (Pacific Grove, California, Hiatt 1948) and May to November (Sea Beach, California, Schlotterbeck 1976; Puls 2001), but off-season mating occurs (Ricketts and Calvin 1971). Most breeding, however, takes place in summer months (Booolootian et al. 1959). Impregnation to extrusion of eggs takes 16–25 days with incubation period averaging 29 days. Mating generally occurs once a year and occasionally second broods are produced (Hiatt 1948). Upon hatching embryos are deep purple brown in color (Schlotterbeck 1976). The reproduction and life-cycle of the parasitic nemertean, *C. epialti* is dependent on and corresponds to that of its host species. However, this nemertean is not host specific (unlike *Carcinonemertes errans* on *Cancer magister*) and occurs amongst egg masses of other species including *H. nudus*, *H. oregonensis* (Kuris 1993; Roe et al. 2007; Kuris et al. 2007).

Larva: Larval development in *P. crassipes* proceeds via a prezoa and a series of zoea (five total) and megalopa stages, each marked by a molt with total larval duration (to fifth zoea, as measured in the lab) of approximately 95 days (described by Schlotterbeck 1976). The zoea are planktotrophic and have large compound eyes and four spines: one each dorsal and rostral and two lateral (see Fig. 2–11, Schlotterbeck 1976; Fig. 32, Puls 2001; Fig. 54.5, Martin 2014). The rostrum and dorsal spines are of equal length and the two lateral spines are shorter (Puls 2001). The first zoeal stage lasts 18 days, the second 22 days, the third 21 days, the fourth 25 days and the final stage lasts 29 days (Schlotterbeck 1976). In *P. crassipes*, the lateral spines are not present until the second zoea stage. The first zoea has no exospines on the telson, is approximately 1.0 mm (measured from tip of rostrum to tip of telson) and has lateral knobs on the second and third segments, where *H. oregonensis* has lateral knobs on only the second segment (Puls 2001). The zoea of *Hemigrapsus* species and *P. crassipes* can be differentiated by body and eye size (Schlotterbeck 1976).

Pachygrapsus crassipes megalopae have a square carapace and, at 5.6 mm in length and 2.7 in width, are much larger than that of *Hemigrapsus*. Megalopae are transparent and with telson bearing two long medial spines and several short ones (Fig. 4) (Hiatt 1948; Fig. 33, Puls 2001). Developmental time to megalopa stage is approximately six weeks and pelagic larvae may be transported shoreward in surface slicks associated with internal waves (Shanks 1983, 1985).

Juvenile: Juveniles alert and quick, are especially long-legged and have large eyes. At sexual maturity female carapace width is 15 mm and males is 12 mm (Hiatt 1948).

Longevity: Probably about three years (Hiatt 1948).

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007). Female *P. crassipes* reach sexual maturity (to 15 mm wide) after 11–12 months and males in 7 months (about 12 mm) (Hiatt 1948).

Food: Mostly herbivorous, scrapes off algal film (*Fucus*, *Ulva*) with excavated chelae (Hiatt 1948; Kozloff 1993) and also eats detritus or other live animals. Perception of food is by visual, chemical and tactile stimuli, but not by odor. Feeds diurnally as well as nocturnally (Hiatt 1948), and chiefly in tide pools (Bovbjerg 1960b).

Predators: Gulls, rats, other *Pachygrapsus* (while soft), and large anemones (*Bunodactis*, *Anthopleura*) which can capture small animals. Because they are nocturnal and fast, *Pachygrapsus* are not bothered by most birds (Hiatt 1948).

Behavior: Mud dwellers that are seldom more than 4–5 feet from their home hole (Morgan et al. 2006). Pugnacious, solitary, active and move easily and quickly in any direction. Poor swimmers (Hiatt 1948). Aggregate in crevices well above the water in daylight (Bovbjerg 1960b).

Bibliography

1. BOOLOOTIAN, R. A., A. C. GIESE, A. FARMANFAMAIAN, and J. TUCKER. 1959. Reproductive cycles of five west coast crabs. *Physiological Zoology*. 32:213-220.
2. BOVBJERG, R. V. 1960a. Behavioral ecology of the crab, *Pachygrapsus crassipes*. *Ecology*. 41:668-672.
3. —. 1960b. Courtship behavior of the lined shore crab, *Pachygrapsus crassipes* Randall. *Pacific Science*. 14:421-422.
4. CASSONE, B. J., and E. G. BOULDING. 2006. Genetic structure and phylogeography of the lined shore crab, *Pachygrapsus crassipes*, along the northeastern and western Pacific coasts. *Marine Biology*. 149:213-226.
5. GROSS, W. J. 1959. The effect of osmotic stress on the ionic exchange of a shore crab. *Biological Bulletin*. 116:248-257.
6. GROSS, W. J., and L. A. MARSHALL. 1960. The influence of salinity on the magnesium and water fluxes of a crab. *Biological Bulletin*. 119:440-453.
7. HIATT, R. W. 1948. The biology of the lined shore crab *Pachygrapsus crassipes* Randall. *Pacific Science*. 2:135-213.
8. JONES, L. 1941. Osmotic regulation in several crabs of the Pacific coast of North America. *Journal of Cellular and Comparative Physiology*.
9. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
10. KURIS, A. M. 1993. Life cycles of nemerteans that are symbiotic egg predators of decapod crustacea: adaptations to host life histories. *Hydrobiologia*. 266:1-14.
11. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
12. MARTIN, J. W. 2014. Brachyura, p. 295-310. *In: Atlas of crustacean larvae*. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
13. MORGAN, S., S. SPILSETH, H. PAGE, A. BROOKS, and E. GROSHOLZ. 2006. Spatial and temporal movement of the lined shore crab *Pachygrapsus crassipes* in salt marshes and its utility as an indicator of habitat condition. *Marine ecology. Progress series*. 314:271-281.
14. NG, P. K. L., D. GUINOT, and P. J. F. DAVIE. 2008. Systema brachyurorum: Part I. Annotated checklist of the extant Brachyuran crabs of the world. *Raffles Bulletin of Zoology Supplement*. 17:1-286.
15. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
16. RATHBUN, M. J. 1918. The grapsoid crabs of America. *Bulletin of the United States Natural Museum*. 97:128-145.
17. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
18. ROE, P., J. L. NORENBURG, and S. MASLAKOVA. 2007. Nemertea, p. 221-233. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
19. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*. Thomson Brooks/Cole, Belmont, CA.
20. SAMMY DE GRAVE, N., D. PENTCHEFF, and S. T. AHYONG. 2009. A classification of living and fossil genera of decapod crustaceans. *Raffles Bulletin of Zoology*:1-109.
21. SCHLOTTERBECK, R. E. 1976. Larval development of the lined shore crab, *Pachygrapsus crassipes* Randall, 1840. (Decapod: Brachyura: Grapsidae) reared in the laboratory. *Crustaceana*. 30:184-200.

22. SCHMITT, W. L. 1921. The marine decapod crustacea of California. University of California Publications in Zoology. 23:1-470.
23. SCHUBART, C. D. 2011. Reconstruction of phylogenetic relationships within Grapsidae (Crustacea: Brachyura) and comparison of trans-isthmian versus amphi-atlantic gene flow based on mtDNA. Zoologischer Anzeiger. 250:472-478.
24. SCHUBART, C. D., J. A. CUESTA, R. DIESEL, and D. L. FELDER. 2000. Molecular phylogeny, taxonomy, and evolution of non-marine lineages within the American grapsoid crabs (Crustacea: Brachyura). Molecular Phylogenetics and Evolution. 15:179-190.
25. SHANKS, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Marine Ecology Progress Series. 13:311-315.
26. —. 1985. Behavioral basis of internal wave induced shoreward transport of megalopae of the crab *Pachygrapsus crassipes*. Marine Ecology Progress Series. 24:289-295.
27. SHIELDS, J. D., and A. M. KURIS. 1988. Temporal variation in abundance of the egg predator *Carcinonemertes epialti* (Nemertea) and its effect on egg mortality of its host, the shore crab, *Hemigrapsus oregonensis*. Hydrobiologia. 156:31-38.
28. SYMONS, P. E. K. 1964. Behavioral responses of the crab *Hemigrapsus oregonensis* to temperature, diurnal light variation, and food stimuli. Ecology. 45:580-591.
29. VON STERNBERG, R., and N. CUMBERLIDGE. 1998. Taxic relationships within the Grapsidae MacLeay, 1838 (Crustacea: Decapoda: Eubrachyura). Journal of Comparative Biology. 3:115-136.
30. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

Rhithropanopues harrisii

A mud crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Brachyura
Family: Panopeidae

Taxonomy: The large and taxonomically problematic family, Xanthidae was divided into eight smaller families by Guinot (1978). This included Panopeidae, to which *R. harrisii* belongs, and Pilumnidae (*Pilumnus*) placing emphasis on more discrete characters (e.g. pleopod morphology) than previously used (e.g. carapace and chelae morphology) (Martin and Abele 1986; Schubart et al. 2000). *Rhithropanopeus* was separated from *Panopeus* based on unique pleopod morphology (Martin and Abele 1986). Thus, known synonyms previously used for *R. harrisii* include *Panopeus wurdemannii* and *Pilumnus harrisii* (Wicksten 2012).

Description

Size: Male carapace generally 16 mm in length and female carapaces are usually 12 mm in length (Wicksten 2012). Type specimen was 19 mm (Rathbun 1930), and among Coos Bay specimens 36% (both sexes) measured at least 6 mm in width (Pisciotta 1977) and males were larger than females (Ryan 1956). Weight rarely over four grams (San Francisco Bay, Smith 1967).

Color: Dull green to brown dorsally, pale white ventrally. Dactyls whitish (Rathbun 1930; see Fig. in Wicksten 2012).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are reduced and folded ventrally (Decapoda, Kuris et al. 2007).

Cephalothorax:

Eyes: Frontal and fill orbits.

Antennae:

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The

maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004).

Carapace: Sub-quadrate, almost trapezoidal and wider than long. Carapace sides converge slightly. Front truncate and posterior broad with greatest width at fourth lateral tooth (Ryan 1956). Prominent horizontal dorsal ridges (Rathbun 1930) (Fig. 1) (Ryan 1956).

Frontal Area: Front truncate and less than a third as wide as carapace. Frontal margin straight, double-edged, channeled and thick with a triangular median notch (Figs. 1, 2).

Teeth: Five carapace teeth. The first, antero-lateral tooth fused with the postorbital angle and followed by 2–3 anterolateral teeth. Last three teeth are dentate, pointing forward with the last tooth smallest (Fig. 2) (Wicksten 2012).

Pereopods: Long, slender compressed and covered with fine hairs (Fig. 1).

Chelipeds: Unequal, heavy, with short fixed finger and curved dactyl. Minor chelae with longer fixed finger and dactyl. Carpus with internal tooth (Wicksten 2012). Chelae smooth (older individuals), or with lines and granules (young individuals) (Fig. 4).

Abdomen (Pleon): Male abdomen narrow (see **Sexual Dimorphism**) with five segments with third segment not contiguous with coxa of the last pair of legs (Fig. 3). Terminal segment rounded (Fig. 3) (Rathbun 1930).

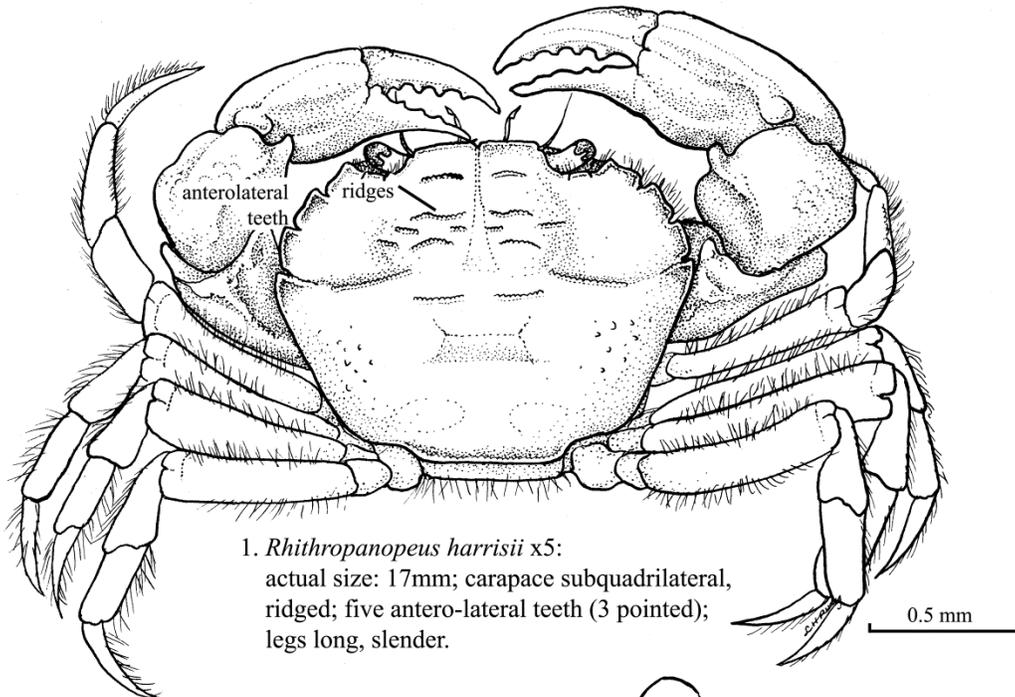
Telson & Uropods:

Sexual Dimorphism: Male and female brachyuran crabs are generally easy to differentiate. The most conspicuous feature, the abdomen, is narrow and triangular in males while it is wide and flap-like in females (Brachyura, Kuris et al. 2007).

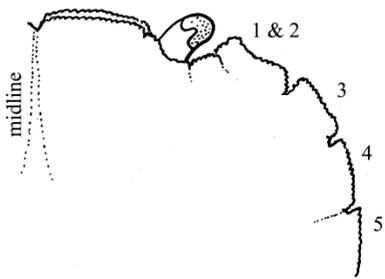
Possible Misidentifications

Two panopeid genera occur locally; *Rhithropanopeus* and *Lophopanopeus* (Kuris et al. 2007). *Rhithropanopeus*, currently

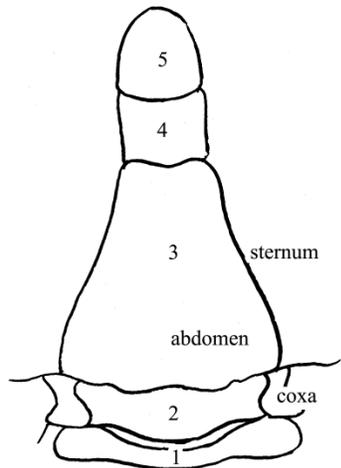
Rhithropanopeus harrisii



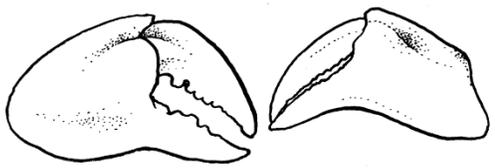
1. *Rhithropanopeus harrisii* x5:
actual size: 17mm; carapace subquadrilateral,
ridged; five antero-lateral teeth (3 pointed);
legs long, slender.



2. Carapace (right frontal):
frontal edge straight, double-edged;
triangular median notch; eyes fills
orbit; teeth 1,2 coalesced; 3,4,5 dentate.



3. Abdomen (Male):
narrow; segment three not contiguous
with coxae of legs.



4. Chelae (Male):
heavy, unequal; white, smooth
(after Benedict, Rathbun).

monotypic, is characterized by unique pleopod morphology, particularly the lack of a lateral tooth. Additional characters include a median process that is rounded and with one long central spine and 3–4 long spines laterally (Martin and Abele 1986). Furthermore, *R. harrisii* has white dactyls (or fingers) while local members of *Lophopanopeus* have black dactyls and are not found in brackish water (Kuris et al. 2007). Additional characters of the genus *Lophopanopeus* include tri-lobed pleopods with accessory processes extending acutely from the main shaft, a medial lobe that is deeply furrowed and a simple lateral tooth (Martin and Abele 1986). The two local species can be differentiated by the distal segments of ambulatory legs that are hairy in *L. bellus* and smooth in *L. leucomanus* (Kuris et al. 2007).

Rhithropanopeus can also be mistaken for the shore crab, *Hemigrapsus oregonensis*, but *Rhithropanopeus* has strong dorsal ridges, three side spurs (Ricketts and Calvin 1971) (last three pointed antero-lateral teeth), slightly convergent sides and long, slender legs. *Rhithropanopeus harrisii* sometimes competes for food with *H. oregonensis* in the lower parts of bays where they can co-occur.

Ecological Information

Range: Type locality is the Cambridge Marshes and the Charles River, Massachusetts (Wicksten 2012). Native to the Gulf of St. Lawrence, Canada to Veracruz, Mexico and introduced to northern Europe (e.g. Holland) and the west coast of North America (San Francisco and Coos Bay) in 1940 (Garth and Abbott 1980; Puls 2001; Wicksten 2012).

Local Distribution: Probably introduced to San Francisco, California with eastern oyster spat (*Crassostrea virginica*) in 1940 and expanded northward to Coos Bay, Oregon (Ricketts and Calvin 1971). Oregon distribution includes Haynes Inlet, Coos River (Pisciotta 1977), Netarts Bay (Stout 1976) and Yaquina Bay (Pisciotta 1977).

Habitat: Sloughs, under rocks and in mud banks of estuaries, where it burrows (Puls 2001; Kuris et al. 2007). Tolerates a diversity of conditions (see **Salinity** and **Temperature**), but prefers some kind of

shelter (e.g. oyster beds, Chesapeake Bay, Ryan 1956).

Salinity: Euryhaline and tolerant of a wide range in salinity, usually brackish to freshwater (Rathbun 1930; Garth and Abbott 1980; Pisciotta 1977; Forward 2009). This species osmoregulates very effectively, increasing excretion of urine in dilute waters and adjusting the permeability of the body wall (Garth and Abbott 1980). Adult salinity tolerance is generally between 0–18, but can range to salinities of up to 40 (Forward 2009). Larvae develop normally (in lab) at salinities of 5–35, while no larvae survive at salinities less than 1 (Costlow et al. 1966). Additionally, zoeae were found in salinities of 4–23.5 (greatest number at 15, Bousfield 1955). It is thought that tolerance of lower salinities is the result of reproductive refuge from the rhizocephalan parasite, *Loxothylaxus panopaei*, that settles onto *R. harrisii* larvae at salinities above 10 (Forward 2009). This parasite is currently only present in Chesapeake Bay on the east coast, and the Gulf of Mexico, where infection rates are affected by salinity and spatial separation between host populations (Grosholz and Ruiz 1995).

Temperature: Adults and larvae tolerant of a wide temperature range, from 7° to 35° C (Costlow et al. 1966; Vernberg and Vernberg 1972; Forward 2009). Temperature range unknown for planktonic larvae (Costlow et al. 1966), but their retention in the estuary (rather than moving offshore) suggests a wide tolerance (Forward 2009). Found in Coos Bay at temperatures ranging from 9–16° (October to December, Pisciotta 1977).

Tidal Level: High intertidal to depths of approximately 37 m (Wicksten 2012).

Associates: Parasitic rhizocephalan, *Loxothylaxus panopaei*, infests *R. harrisii* in regions where salinity is higher than 10. The *L. panopaei* cyprids settle on *R. harrisii* megalopae (Forward 2009).

Abundance: Can be the dominant species and is found in nearly every arm of Chesapeake Bay, but only occurs in widely scattered patches (where it is abundant) in Oregon estuaries (Ryan 1956; Kuris et al. 2007).

Life-History Information

Reproduction: Reproductive timing varies with latitude. Individuals in northern latitudes are reproductive from July–August, those in mid-latitude from April–September and southern individuals from April–November (Forward 2009). In Chesapeake Bay, females are ovigerous in summer and early fall (Ryan 1956). Females do not migrate to more saline waters to release larvae (Costlow et al. 1966). In regions with a diurnal tidal cycle, larvae are released two hours following high tide, presumably to reduce larval exposure to the low salinity environment of adults, as the tide is not to enable larvae to move offshore as is seen in other brachyurans (Forward 2009).

Larva: The larvae and larval biology of *R. harrisii* are well described (Connolly 1925; Costlow and Bookhout 1971; Forward 2009; Marco-Herrero et al. 2014). Larval development in *R. harrisii* proceeds via a prezoaea, several zoea (four total) and a final megalopae stage, each marked by a molt (Jaffe et al. 1987; Puls 2001; Forward 2009). The zoea are planktotrophic and have large compound eyes and four spines: one each dorsal and rostral and two lateral (see Fig. 54.5, Martin 2014). The rostrum is longer than the dorsal spine (Connolly 1925; Puls 2001) and lateral spines on the distal ends of the fifth abdominal segments are very long (Connolly 1925). Larval size at each of four stages is outlined in Connolly (1925). Megalopae are 1.1 x 1.0 mm (Connolly 1925; Puls 2001; see Fig. 54.9, Martin 2014), have a carapace with uneven surface and rostrum with median triangular tooth, as seen in adults (see **Frontal Area**) (Connolly 1925). Wild-caught megalopae identified using DNA sequence data were described by Marco-Herrero et al. in 2014. The megalopae of *R. harrisii* are unique among panopeids in lacking horns at the rostrum base. Other differentiating characters include the number of segments of the antennular flagellum (six in *R. harrisii*) and the absence of a recurved spine on the cheliped ischium (for typical panopeid spine see Fig. 54.7, Martin 2014). Unique to *R. harrisii*, larvae do not move offshore and, instead, are retained near the adult population within the estuary by vertically migrating within the water column (ascend during flood and descend during ebb tides) (Forward 2009). Larva settlement is

accelerated by chemical cues from conspecifics, biofilms, estuarine water, humic acids and prey odor. Metamorphosis times are reduced with reducing salinity (Fitzgerald et al. 1998). Conversely, settlement is reduced by predator chemical cues, hypoxia and increasing ammonia/ammonium concentrations (Forward 2009).

Juvenile: Can be recognized by their granulated chelae.

Longevity: Less than two years (Grosholz and Ruiz 1995).

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007). Experiments in *R. harrisii* showed that eyestalk removal increased growth rate up to two times and that growth resulted from cell proliferation, not enlargement (Freeman et al. 1983). Sexual maturity in *R. harrisii* is probably reached during the second summer and the total number of juvenile in-stars (molts) is not known (Ryan 1956).

Food: Algae and small crabs (sometimes including juvenile conspecifics).

Rhithropanopeus harrisii is a nocturnal feeder.

Predators:

Behavior: Xanthid and panopeid crabs are generally slow-moving, inactive crabs, sometimes playing dead when disturbed (Kuris et al. 2007). *Rhithropanopeus harrisii* hides under rocks and is less active than *Hemigrapsus oregonensis*, with which it co-occurs.

Bibliography

1. BOUSFIELD, E. L. 1955. Ecological control of the occurrence of barnacles in the Miramichi Estuary. Bulletin of the National Museum of Canada. 137:1-69.
2. CONNOLLY, C. J. 1925. The larval stages and megalops of *Rhithropanopeus harrisii* (Gould). Contributions to Canadian Biology (NS). 2:327-33.

3. COSTLOW, J. D., C. G. BOOKHOUT, and R. J. MONROE. 1966. Studies of the larval development of the crab, *Rhithropanopeus harrisi*: I. The effect of salinity and temperature on larval development. *Physiological Zoology*. 39:81-100.
4. COSTLOW, J. D. J., and C. G. BOOKHOUT. 1971. The Effect of cyclic temperatures on larval development in the mud crab *Rhithropanopeus harrisi*, p. 211-220. *In: Fourth European marine biology symposium*. D. J. Crisp (ed.). Cambridge University Press, New York.
5. FITZGERALD, T. P., R. B. FORWARD, and R. A. TANKERSLEY. 1998. Metamorphosis of the estuarine crab *Rhithropanopeus harrisi*: effect of water type and adult odor. *Marine Ecology Progress Series*. 165:217-223.
6. FORWARD, R. B. J. 2009. Larval biology of the crab *Rhithropanopeus harrisi* (Gould): a synthesis. *Biological Bulletin*. 216:243-256.
7. FREEMAN, J. A., T. L. WEST, and J. D. COSTLOW. 1983. Post larval growth in juvenile *Rhithropanopeus harrisi*. *Biological Bulletin*. 165:409-415.
8. GARTH, J. S., and D. P. ABBOTT. 1980. Brachyura: the true crabs, p. 594-630. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
9. GROSHOLZ, E. D., and G. M. RUIZ. 1995. Does spatial heterogeneity and genetic variation in populations of the Xanthid crab *Rhithropanopeus harrisi* (Gould) influence the prevalence of an introduced parasitic castrator? *Journal of Experimental Marine Biology and Ecology*. 187:129-145.
10. GUINOT, D. 1978. Principles of an evolutive classificaton of Brachyura-Decapoda-Crustacea. *Bulletin Biologique de la France et de la Belgique*. 112:211-292.
11. JAFFE, L. A., C. F. NYBLADE, R. B. FORWARD, and S. SULKIN. 1987. Phylum or subphylum Crustacea, class Malacostraca, order Decapoda, Brachyura, p. 451-475. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
12. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
13. MARCO-HERRERO, E., J. IGNACIO GONZALEZ-GORDILLO, and J. A. CUESTA. 2014. Morphology of the megalopa of the mud crab, *Rhithropanopeus harrisi* (Gould, 1841) (Decapoda: Brachyura: Panopeidae), identified by DNA barcode. *Helgoland Marine Research*. 68:201-208.
14. MARTIN, J. W. 2014. Brachyura, p. 295-310. *In: Atlas of crustacean larvae*. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
15. MARTIN, J. W., and L. G. ABELE. 1986. Notes on male pleopod morphology in the Brachyuran crab family Panopeidae Ortmann, 1893, *Sensu Guinot (1978) (Decapoda)*. *Crustaceana*. 50:182-198.
16. PISCIOTTO, R. J. 1977. The distribution of *Rhithropanopeus harrisi* in Coos Bay. *Oregon Institute of Marine Biology (University of Oregon)*.
17. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
18. RATHBUN, M. J. 1930. The Cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. U.S. Government Printing Office, Washington, D.C.
19. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
20. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. *Invertebrate*

- zoology: a functional evolutionary approach. Thomson Brooks/Cole, Belmont, CA.
21. RYAN, E. P. 1956. Observations on the life histories and distribution of the Xanthid crabs of Chesapeake Bay. *American Midland Naturalist*. 56:138-162.
 22. SCHUBART, C. D., J. E. NEIGEL, and D. L. FELDER. 2000. Molecular phylogeny of mud crabs (Brachyura: Panopeidae) from the northwestern Atlantic and the role of morphological stasis and convergence. *Marine Biology*. 137:11-18.
 23. SMITH, R. I. 1967. Osmotic regulation and adaptive reduction of water permeability in a brackish-water crab, *Rhithropaneus harrisii*. *Biological Bulletin*. 133:643-658.
 24. STOUT, H., and S. V. SHABICA. 1976. The natural resources and human utilization of Netarts Bay, Oregon. Oregon State University, Corvallis, Oregon.
 25. VERNBERG, W. B., and V. F.J. 1972. Environmental physiology of marine animals. Springer-Verlag, New York.
 26. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

Pinnixa faba

A pea crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Brachyura
Family: Pinnotheridae

Description

Size: Female *P. faba* are much larger than males. Females are about 20 mm in width while males are 10 mm wide (Fig. 1). Average first true crab size is 1.54 mm (Pearce 1966).

Color: Grayish tan with orange or rust colored markings. Immature crabs are white, eggs orange and female cheliped tips are white. Individuals are bright orange just after molting (Pearce 1966).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are reduced and folded ventrally (Decapoda, Kuris et al. 2007).

Cephalothorax:

Eyes: Orbits oval and eyestalks very short. In males, the eyes fill orbits (Fig. 4) (Rathbun 1918).

Antennae:

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004). In *P. faba*, external maxillipeds have a large, separate merus (the arm) and ischium (the first large article of the maxilliped). The carpus articulates at the outer angle of the merus and a palp articulates at the inner proximal end of the merus. Exognath is with several joints and is hidden (Rathbun 1918).

Carapace: Carapace is smooth, rounded, swollen and oblong with no strong post- or anterolateral ridges. Carapace is 1.6–1.9 times wider than long and sides are truncate, slope steeply and meet at an angle (Fig. 1) (Zmarzly 1992). Male carapaces

sometimes have a vertical, compressed lobe at the anterolateral angle (Fig. 4).

Frontal Area: Narrow, slightly advanced in males and strong medial groove in females (Figs. 4, 1).

Teeth: No anterolateral teeth.

Pereopods: The merus of males third walking leg is more than twice as long as wide (Fig. 4). Dactyli of both sexes are short and strongly curved (less so in fourth dactyl) (Zmarzly 1992). The third walking legs are longest and all legs are similar in shape, except the merus of the first leg in males, which is concave above, not convex as are others. Female legs more alike than in males.

Chelipeds: Chelae are large, smooth and about 2/3 width of carapace (Zmarzly 1992). Pollex (thumb or fixed finger) straight and a little shorter than movable dactyl, which is curved (Fig. 3). Dactyls of female are white-tipped and not gaping (Rathbun 1918) (Fig. 3a). Male chelae manus (palm) are almost oblong, widening at tip, pollex shorter than dactyl, which is curved, and has a tooth at its base (Fig. 3b). The male dactyl is hairy within (Fig. 3b) (Zmarzly 1992).

Abdomen (Pleon): Consisting of seven free somites in both sexes (Zmarzly 1992). Male abdomen is narrow with last segment rounded and the next to last segment constricted in middle (Fig. 5b). Female abdomen is very broad (Fig. 5a).

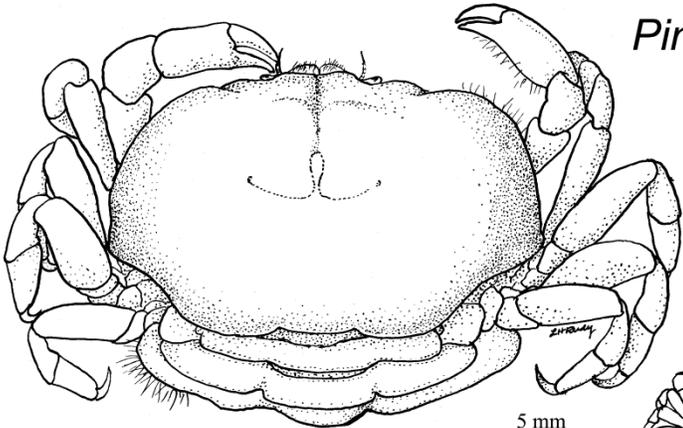
Telson & Uropods:

Sexual Dimorphism: Male and female brachyuran crabs are easily differentiable. The most conspicuous feature, the abdomen, is narrow and triangular in males while it is wide and flap-like in females (Brachyura, Kuris et al. 2007). Female *P. faba* are larger than males, have slightly different general body shape and chelae morphology (see above).

Possible Misidentifications

All members of the Pinnotheridae are small, have a wide, rounded carapace, small eyes and short eyestalks. Pea crabs are very particular to a specific habitat and/or host.

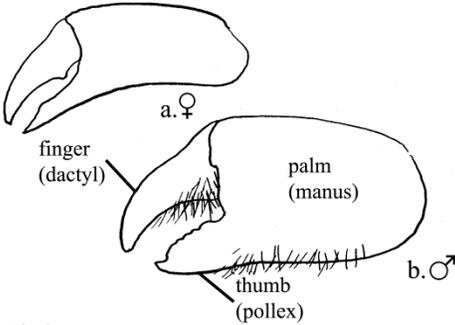
Pinnixa faba



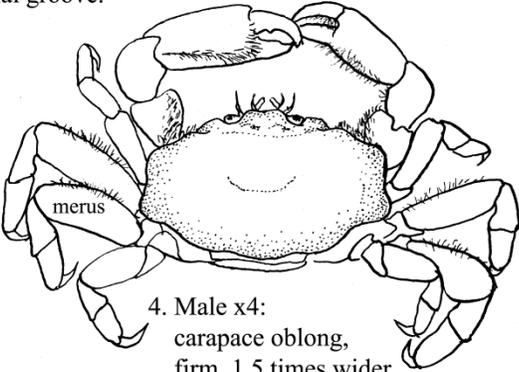
1. *Pinnixa faba* (female) x4:
actual size 2 cm; carapace rounded,
swollen; eyes, orbits small and oval;
frontal area: medial groove.



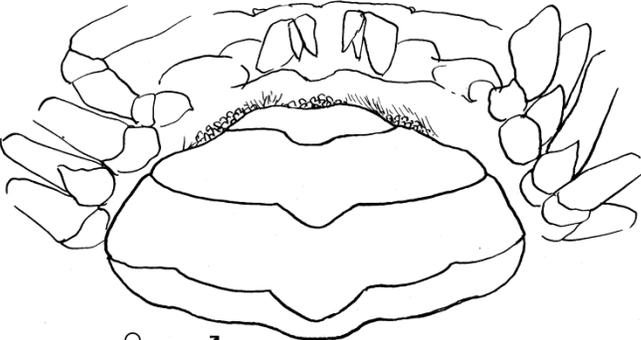
2. Immature x4



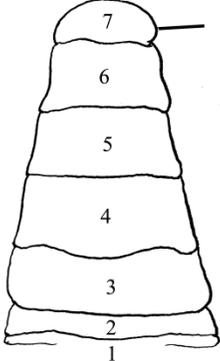
3. Chelae x7:
a. female: white, not gaping
b. male: thumb straight; dactyl curved,
toothed; fingers hairy; palm widens distally.



4. Male x4:
carapace oblong,
firm, 1.5 times wider
than long; sides slope steeply, antero- and
post-lateral margins meet at angle; merus
long (third walking leg).



5. Abdomens, ♀ and ♂:
a. female: seven-jointed, very wide



b. male: narrow; last
segment rounded.

There are 15 pinnotherid species reported from central California to Oregon and most of them are in the genus *Pinnixa* (Kuris et al. 2007). A thorough key to local members of the genus *Pinnixa* was published by Zmarzly (1992). The genus is characterized by a carapace wider than long, frontal margin with median groove, short eyestalks with orbits ovate and filled by eyes, third maxillipeds with small ischium, large merus and large palp, third walking leg longer and more robust than others and abdomen with seven free somites (Zmarzly 1992). There are 11 local species (Kuris et al. 2007). *Pinnixa faba* can be differentiated by chelae morphology where the pollex in males is straight with an inner dactyl margin bearing a single triangular tooth (Fig. 3b). Female chela morphology also has straight pollex and opposing fingers that meet tightly, with no gape (Zmarzly 1992).

The closely related *Pinnixa littoralis*, is often found in the clam *Tresus capax*, as is *P. faba*. *Pinnixa littoralis* is distinguishable by its carapace, which is pointed at the sides and the merus of its third walking leg is twice as long as wide (in males), but not longer as in *P. faba*. The female fingers gape, her walking legs are rather alike and the male pollex is deflexed (bent down) and the movable finger (dactyl) has no tooth at its base. The two species also differ in color: *P. littoralis* females are greenish-yellow. Both these species are found in pairs, not singly as with most pea crabs (Pearce 1966).

Other *Pinnixa* species are *P. longipes*, with exceptionally large third walking legs, commensal with tube worms; *P. barnharti*, which is commensal with a holothurian; *P. occidentalis*, with cylindrical fourth and fifth walking legs, found in echiuroid worm burrows and associated with *P. franciscana*, *P. tubicola*, and *P. schmitti*, species also found in worm burrows and tubes. The carapace has a granular cardiac ridge, curved teeth along the anterolateral margin and a conspicuous subhepatic tooth in *P. scamit*. Little is known about the final species, *P. weymouthi* (Kuris et al. 2007).

The other local pinnotherid genera include *Pinnotheres* (symbiotic with oysters), *Parapinnixa* (symbiotic with polychaetes *Terebella californica* and *Loimia*), *Fabia* (symbiotic with bivalves, especially *Mytilus*) *Opisthopus* (symbiotic with various molluscs including *Tresus*, and some holothurians).

Scleroplax granulata, found usually with mud and ghost shrimp, has a wide carapace like *P. faba*, but its antero- and posterolateral margins curve gradually, not forming an angle.

Ecological Information

Range: Type locality is Puget Sound, Washington. Known range includes Alaska to Mexico (Fig. 1, Zmarzly 1992).

Local Distribution: In clams found in bay mud, or mud and sand.

Habitat: Heavily infests *Tresus capax*, the gaper clam, (nearly 100% in Puget Sound individuals). Adult *Pinnixa* are rarely found in *Tresus nuttalli* when *T. capax* and *T. nuttalli* co-occur, however, south of *T. capax*'s range *P. faba* occupies *T. nuttalli*. *Tresus capax* is likely preferred because female *P. faba* attach to the visceral fold of their host which is present in *T. capax* and not in *T. nuttalli* (Zmarzly 1992). *Pinnixa faba* inhabits *Tresus* in pairs. The large female clings to the visceral fold in the mantle cavity of the clam and remains there, immobile, and permanently close to the food supply. Smaller males and immature crabs are found throughout the mantle cavity and around the incurrent siphon, although they are often close to the female. The young crabs seem to be free-living. The clam, *Tresus*, is found in mud or sandy mud, 25–60 cm below the surface. *Pinnixa faba* individuals are also found in *Saxidomus*, *Mya*, *Tapes*, *Macoma*, and as immature crabs, in *Clinocardium* (Rathbun 1918). It is found in the invasive manila clam (*Venerupis philippinarum*) and invasive varnish clam (*Nuttalia obscurata*) (Marshall et al. 2003). Individuals also reported in non-bivalve hosts such as abalone, sea cucumbers, limpets, sea hares, and tunicates (Schmitt 1921; Hart 1982).

Salinity: Host, *Tresus capax*, found at salinities from 30.5–33.5 (Humboldt Bay, California).

Temperature:

Tidal Level:

Associates: Female *P. faba* are never free-living and the males (and immature individuals) move about only occasionally. The pea crab is always found living parasitically in a bivalve. Very occasionally an immature crab of another species (*P. littoralis*) will inhabit the same clam (Pearce 1966). Blisters and irritation of the clam's

viscera are noticeable where the female is lodged (Kozloff 1993). The crab is parasitic, not commensal – it steals food from the clam, and apparently gives nothing in return. Fossils from Cape Blanco, Oregon suggest that *P. faba* and *T. capax* have had a symbiotic relationship for at least 33,000 years (Zullo and Chivers 1969).

Abundance: Can be very prevalent in certain clam populations (almost 100% infestation) but prevalence varies with season (Pearce 1966).

Life-History Information

Reproduction: All decapod crustacean females attach recently laid gelatinous egg masses to their pleopods. The outer embryo membrane thickens and a strand develops that attaches each embryo to pleopod setae (Decapoda, Kuris et al. 2007). *Pinnixa faba* can have two broods per year (occurring one month later than in *P. littoralis*), the first in late spring to summer and the second in winter to early spring. The period between the two broods may or may not be punctuated by a molt (Pearce 1966; Jaffe et al. 1987). Copulation occurs within the clam, as the female is sessile. Males are usually found on or next to females. One to five immature crabs of both sexes have been found resident in the clam (particularly in summer and falls), presumably waiting to assume adult roles at the death of either of the adult pair. Each female brood contains 7,000–8,000 embryos that hatch between August and September, having a 47-day pelagic duration in the lab (Washington, Jaffe et al. 1987).

Larva: The larvae of pinnotherids proceed through planktonic prezoaea, zoea (two stages) and megalopa stages. The zoea have large compound eyes and four spines: one each dorsal and rostral and two lateral (see Fig. 54.5, Martin 2014). The most definitive feature of pea crab zoea is the fifth abdominal segment, which is expanded laterally (see <http://invert-embryo.blogspot.com/2012/04/identifying-pinnotherid-larvae.html>; Puls 2001). Megalopae have an oval carapace that is wider than long, granular and 1.4 mm wide and 1.1 mm in length. The posterior pereopods of megalopae and juvenile in-stars have dactyls that lack setae (Jaffe et al. 1987; Puls 2001).

Juvenile: Post-megalopae, development proceeds via a series of in-star stages, which are not free-swimming, that were described by Pearce (1966) (Schneider 1993). At the first in-star stage, the carapace width is approximately 1.5 mm and by the terminal in-star stage it is 20 mm (females at 23–24th in-star) and 10 mm (males at fifteenth in-star) (Pearce 1966). Juvenile *P. faba* and *P. littoralis* are indistinguishable (Zmarzly 1992).

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: Female steal food from host (diatoms, etc.) using mucus strings. Male feeding habits are unknown (Kozloff 1993).

Predators:

Behavior: Young (first true crab stage) crabs infest young *Tresus* when they have just settled out, and remain permanently. Other immature crabs may be found later with this pair. Neither sex is adapted for permanent free-living, nor is the immature crab, which is white, thin and fragile (Pearce 1966).

Bibliography

1. HART, J. F. L. 1982. Crabs and their relatives of British Columbia. British Columbia Provincial Museum Handbook: 1-267.
2. JAFFE, L. A., C. F. NYBLADE, R. B. FORWARD, and S. SULKIN. 1987. Phylum or subphylum Crustacea, class Malacostraca, order Decapoda, Brachyura, p. 451-475. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
3. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British

- Columbia. University of Washington Press, Seattle, WA.
4. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 5. MARSHALL, W. L., S. M. BOWER, and G. R. MEYER. 2003. A comparison of the parasite and symbiont fauna of cohabiting native (*Protothaca staminea*) and introduced (*Venerupis philippinarum* and *Nuttalia obscurata*) clams in British Columbia. *Journal of Shellfish Research.* 22:185-192.
 6. MARTIN, J. W. 2014. Brachyura, p. 295-310. *In: Atlas of crustacean larvae.* J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
 7. PEARCE, J. B. 1966. On *Pinnixa faba* and *Pinnixa littoralis* symbiotica with the clam, *Tresus capax*, p. 565-589. *In: Some contemporary studies in Marine Science.* H. Barnes (ed.). Allen & Unwin, London.
 8. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine invertebrates of the Pacific Northwest.* A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 9. RATHBUN, M. J. 1918. The grapsoid crabs of America. *Bulletin of the United States Natural Museum.* 97:128-145.
 10. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach.* Thomson Brooks/Cole, Belmont, CA.
 11. SCHMITT, W. L. 1921. The marine decapod crustacea of California. *University of California Publications in Zoology.* 23:1-470.
 12. SCHNEIDER, J. A. 1993. The Crab *Pinnixa faba* (Pinnotheridae), in the bivalve *Clinocardium* (*Keenocardium californiense*) (Cardiidae). *Bulletin of Marine Science.* 52:842-843.
 13. ZMARZLY, D. L. 1992. Taxonomic review of pea crabs in the genus *Pinnixa* (Decapoda: Brachyura: Pinnotheridae) occurring on the California shelf, with descriptions of two new species. *Journal of Crustacean Biology.* 12:677-713.
 14. ZULLO, V. A., and D. D. CHIVERS. 1969. Pleistocene symbiosis: Pinnotherid crabs in Pelecypods from Cape Blanco, Oregon. *Veliger.* 12:72-73.

Updated 2015

T.C. Hiebert and L. Rasmuson

Scleroplax granulata

A burrow-dwelling pea crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Brachyura
Family: Pinnotheridae

Taxonomy: The monotypic genus *Scleroplax* was erected for *S. granulata* in 1893 by Rathbun, but its systematic position was controversial until it was recently confirmed, elevated and separated from *Pinnixa* based on characters of the carapace and third maxilliped (Campos 2006).

Description

Size: Up to 11 mm (males) and 12.9 mm (females) in width (California, Garth and Abbott 1980). The illustrated specimen (female from Coos Bay) is 5.5 mm in width (Fig. 1). Males can be larger than females (MacGinitie and MacGinitie 1949), an unusual characteristic among pea crabs.

Color: The illustrated specimen is dark gray with light outlines and red eyes. Males are light tan and orange (Bodega Bay Harbor, CA, Garth and Abbott 1980).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are reduced and folded ventrally (Decapoda, Kuris et al. 2007).

Cephalothorax:

Eyes: Oval and small. Eystalks very short and thick with orbits small.

Antennae:

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004). In *S. granulata* the outer maxillipeds have 3-jointed palps where third article is joined to second proximally, not distally (Fig. 3). A winged extension is present on the merus (Rathbun 1918). Characteristics of the third maxilliped are

taxonomically important for this species. The propodus of the third maxilliped extends to the end of the dactyl rather than in *Pinnixa* where the dactyl extends beyond the short propodus (Campos 2006).

Carapace: Rounded carapace. Oval, smooth, hard, convex and granular. Male carapace smoother than females. Carapace width almost 1½ x length (Kozloff 1974). Antero- and posterolateral edges are rounded and curve to meet gradually, without distinct angles (*Scleroplax*, Rathbun 1918).

Frontal Area: Frontal area entire, blunt, slightly convex with no teeth between eyes.

Teeth:

Pereopods: Legs 2–5 very short (Rathbun 1918), they are slender, somewhat rounded (Kuris et al. 2007) and with slender dactyls. First walking legs are smaller than second while the third is longest (slightly). The fourth walking legs are not greatly smaller than others (Figs. 1, 4).

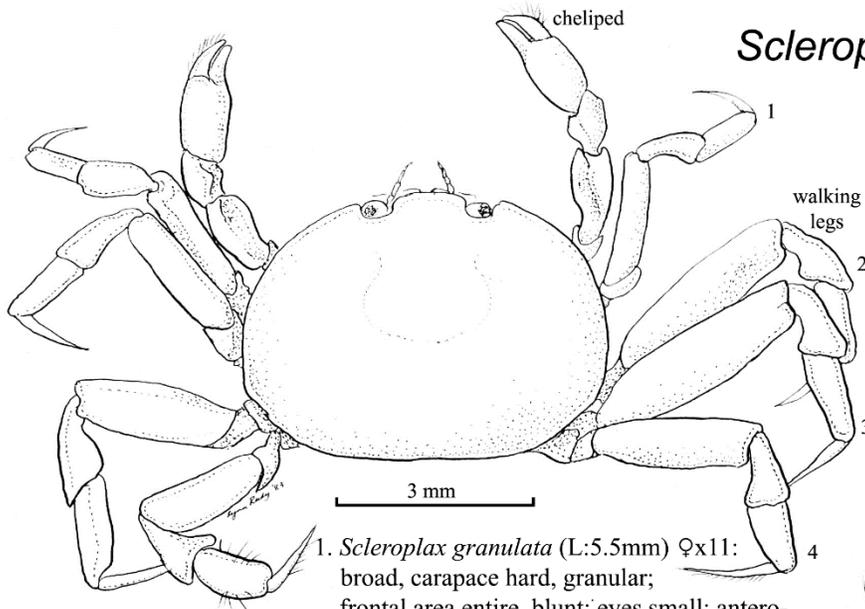
Chelipeds: The chelipeds of females are small, feeble, with thumb horizontal, tip acute and fingers not gaping (Fig. 1). Male chelipeds, on the other hand, are prominent, large and very wide. Their dactyls are curved, smooth, gaping and their propodus is with granulate surface and convex margins. Thumb is shorter than wide and bears one large tooth (Garth and Abbott 1980) (Fig. 2).

Abdomen (Pleon): Female abdomen is wide, smooth, fringed with hair and not reaching beyond sternum (Schmitt 1921). Male abdomen is narrow and tapering gradually (Schmitt 1921) (see *Pinnixa faba*, Fig. 5).

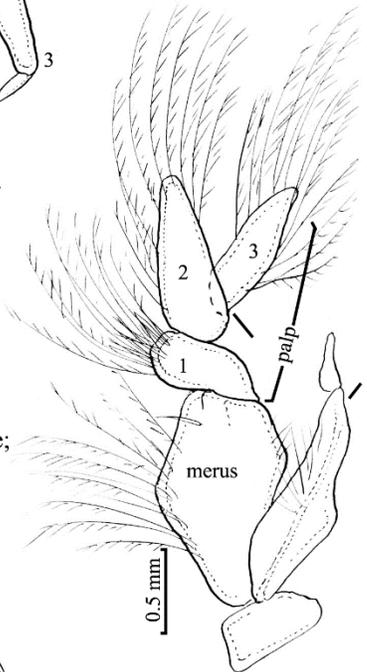
Telson & Uropods:

Sexual Dimorphism: Male and female brachyuran crabs are easily differentiable. The most conspicuous feature, the abdomen, is narrow and triangular in males while it is wide and flap-like in females (Brachyura, Kuris et al. 2007).

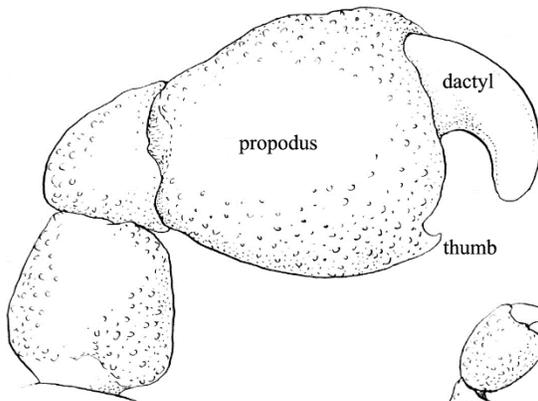
Scleroplax granulata



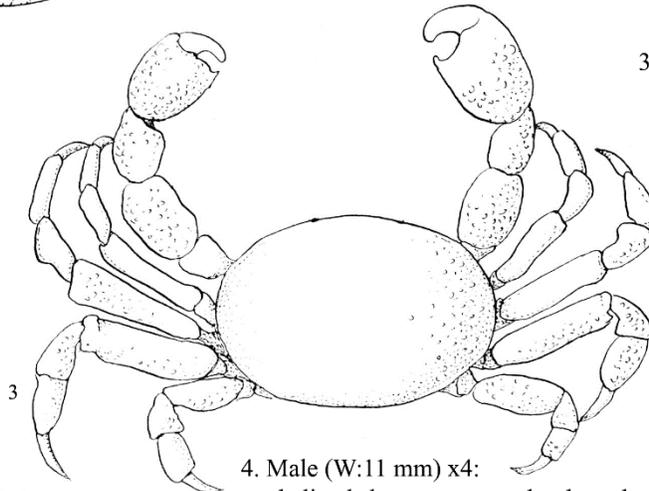
1. *Scleroplax granulata* (L:5.5mm) ♀x11:
broad, carapace hard, granular;
frontal area entire, blunt; eyes small;
antero- and posterolateral edges rounded;
chelipeds feeble, walking legs slender,
rounded, similar.



2. Cheliped ♂ x40:
dactyl curved, fingers gape;
propodus margins convex;
thumb short.



3. Outer maxilliped x28:
palp: 3rd article joined
to 2nd proximally;
winged extension on
merus.



4. Male (W:11 mm) x4:
chelipeds large; carapace hard, oval,
granular; 3rd walking slightly longest
(from Morris et al 1980, Pl. 186).

Possible Misidentifications

All members of the Pinnotheridae are small, have a wide, rounded carapace, small eyes, and short eyestalks. There are 15 pinnotherid species reported from central California to Oregon (Kuris et al. 2007). Pea crabs are very particular to a specific habitat and/or host (see *Pinnixa faba*). The genus *Scleroplax* is monotypic and characterized by a hard, subheptagonal and convex carapace. Additional characters include a third maxilliped with propodus that extends to the end of the dactyl (Campos 2006).

Pinnixa, *Opisthopus* and *Scleroplax* all have a large maxillipedal palps and a wide carapace. *Opisthopus transversus* has a carapace just a little wider than long and walking legs that are sub-equal, the second being slightly longer than the others. Its hosts are nearly always molluscan (Garth and Abbott 1980) and it has not been reported north of Monterey, California (Schmitt 1921).

Most local pea crab species are in the genus *Pinnixa*: *P. littoralis*, is often found in the clam *Tresus capax*; *P. longipes*, with exceptionally large third walking legs, is commensal with tube worms; *P. barnharti*, is commensal with a holothurian; *P. occidentalis*, with cylindrical fourth and fifth walking legs, is found in echiuroid worm burrows and associated with *P. franciscana*, *P. tubicola*, and *P. schmitti*, species also found in worm burrows and tubes. *Pinnixa* species have third walking legs markedly longer than the others (not just slightly longer as in *Scleroplax* (Kuris et al. 2007)) and third maxillipeds with propodus shorter than dactyl (they are of equal length in *Scleroplax*) (Campos 2006). Their carapace is membranous, not hard, and it has a distinctive angle where the antero- and posterolateral carapace margins meet – in contrast to the rounded margins of *Scleroplax*. *Pinnixa franciscana*, a large (to 22 mm wide) crab, with a broad carapace with pointed sides, a sharp line of granules on the cheliped propodus and a widened merus on the third walking legs (Garth and Abbott 1980), are also found in *Neotrypaea* or *Upogebia* burrows with *Scleroplax*. The carapace has a granular cardiac ridge, curved teeth along the anterolateral margin and a conspicuous subhepatic tooth in *P. scamit*. Little is known about the final species, *P.*

weymouthi (Kuris et al. 2007). *Pinnixa schmitti* (Rathbun, 1918) occurs from Alaska to San Francisco Bay (Garth and Abbott 1980). It lives in well-drained loose beach material, not with any particular host (Wells 1940), but in tubes, cavities or burrows within 5 cm of the surface. It has a low tooth on the inner margin of the cheliped dactyl (Kozloff 1974). The dactyls of its fourth walking legs are longer than those of the third pair (Kozloff 1974) and carapace is about 1¾ times wider than long, and tapers laterally, unlike that of *Scleroplax*, which is rounded.

The other local pinnotherid genera include *Pinnotheres* (symbiotic with oysters), *Parapinnixa* (symbiotic with polychaetes *Terebella californica* and *Loimia*), *Fabia* (symbiotic with bivalves, especially *Mytilus*) *Opisthopus* (symbiotic with various molluscs including *Tresus*, and some holothurians). *Parapinnixa* is a southern California genus with a wide carapace, and legs that diminish greatly in size (unlike those of *Scleroplax*).

Ecological Information

Range: Type locality is Ensenada, Baja California, Mexico (Campos 2006). Range includes the north end of Vancouver Island, B.C. south to El Coyote estuary, Punta Abreojos, Baja California Sur, Mexico (Campos 2006; Campos and Campos 2012).

Local Distribution: Coos Bay distribution at several sites. The illustrated specimen is from Jordan Cove (North Spit). Distribution also includes other Oregon estuaries. Attempts to find *S. granulata* in Coos Bay have proven ineffective (Puls 2002).

Habitat: Sandy mud and mudflats of protected bays (Garth and Abbott 1980). Free-living in burrows with *Neotrypaea* (= *Callianassa*) or *Upogebia*, etc. (see **associates**), where it uses protection of burrow, and food and oxygen circulating there. Males migrate between burrows (Garth and Abbott 1980).

Salinity: Occurs with *Neotrypaea*, which is found at salinities from 35–30 (Coos Bay).

Temperature:

Tidal Level: Mid to low intertidal to 55 m (Garth and Abbott 1980; Jaffe et al. 1987).

Associates: *Scleroplax granulata* can be found in burrows of *Neotrypaea* or *Upogebia*. It is also found in the burrows and, sometimes, clinging to the body of the

echiuroid, *Urechis caupo* in the southern part of its distribution. *Scleroplax granulata* is among those pea crabs least intimately associated with its host (Wells 1940) where it is a commensal, not parasitic, species (compare to *Pinnixa faba*). Additional associates include the goby, *Clevelandia ios*, the polynoid polychaete, *Hesperonoe*, which clings to burrow walls to escape *Scleroplax* (MacGinitie and MacGinitie 1949). Bryozoan *Walkeria* lives on legs of *Scleroplax* and bryozoan *Triticella elongata* is on its carapace, appendages and in gill cavities (Garth and Abbott 1980). *Scleroplax* has also been observed with *Mya arenaria* (Friday Harbor, WA, Rathburn 1918).

Abundance: Up to six individuals per burrow, but can also occur singly. *Scleroplax granulata* is the most prevalent of all commensals with *Upogebia* (Garth and Abbott 1980).

Life-History Information

Reproduction: All decapod crustacean females attach recently laid gelatinous egg masses to their pleopods. The outer embryo membrane thickens and a strand develops that attaches each embryo to pleopod setae (Decapoda, Kuris et al. 2007). Egg-bearing female *Scleroplax granulata* have been observed from January to March in California and Oregon (Jaffe et al. 1987). Most larval release occurs at twilight (Rasmuson and Morgan 2013).

Larva: The larvae of pinnotherids proceed through planktonic prezoaea, zoea (two stages) and megalopa stages. The zoea have large compound eyes and four spines: one each dorsal and rostral and two lateral (see Fig. 54.5, Martin 2014). The most definitive feature of pea crab zoea is the fifth abdominal segment, which is expanded laterally (see <http://invert-embryo.blogspot.com/2012/04/identifying-pinnotherid-larvae.html>; Puls 2001). The specific larval morphology of *S. granulata* has not been described.

Juvenile:

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft

shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: Ingests food that falls into burrow and particles brought by goby *Clevelandia*. Also screens material with second maxillipeds (Garth and Abbott 1980).

Predators:

Behavior: Males move around among burrows and are known to exhibit a "possum" posture for up to two minutes if disturbed (Garth and Abbott 1980).

Bibliography

1. CAMPOS, E. 2006. Systematics of the genus *Scleroplax* Rathbun, 1893 (Crustacea: Brachyura: Pinnotheridae). *Zootaxa*. 1344:33-41.
2. CAMPOS, E., and A. DE CAMPOS. 2012. The intertidal brachyuran crabs from estuaries of the west coast Baja California, Mexico (Crustacea: Brachyura). *Marine Biodiversity Records*. 5:1-7.
3. GARTH, J. S., and D. P. ABBOTT. 1980. Brachyura: The True crabs, p. 594-630. *In*: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
4. JAFFE, L. A., C. F. NYBLADE, R. B. FORWARD, and S. SULKIN. 1987. Phylum or subphylum Crustacea, class Malacostraca, order Decapoda, Brachyura, p. 451-475. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
5. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
6. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In*: The Light and Smith manual: intertidal invertebrates from central California to

- Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
7. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 8. MARTIN, J. W. 2014. Brachyura, p. 295-310. *In*: Atlas of crustacean larvae. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
 9. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 10. —. 2002. Transport of zooplankton in South Slough, Oregon. M.S. University of Oregon.
 11. RASMUSON, L. K., and S. G. MORGAN. 2013. Fish predation after weakly synchronized larval release in a coastal upwelling system. *Marine Ecology Progress Series*. 490:185-198.
 12. RATHBUN, M. J. 1918. The grapsoid crabs of America. *Bulletin of the United States Natural Museum*. 97:128-145.
 13. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*. Thomson Brooks/Cole, Belmont, CA.
 14. SCHMITT, W. L. 1921. The marine decapod crustacea of California. *University of California Publications in Zoology*. 23:1-470.
 15. WELLS, W. 1940. Ecological studies on the pinnotherid crabs of Puget Sound. *University of Washington Publications in Oceanography*. 2:19-50.

Updated 2015

T.C. Hiebert and L. Rasmuson

Hemigrapsus nudus

The purple shore crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Brachyura
Family: Varunidae

Taxonomy: The brachyuran family Grapsidae, the shore crabs, was a very large family with several subfamilies and little taxonomic scrutiny, until recently. Based on molecular and morphological evidence, authors (von Sternberg and Cumberlidge 2000; Schubart et al. 2000; de Grave et al. 2009; Schubart 2011) elevated all grapsid subfamilies to family level, reducing the number of species formally within the Grapsidae. Recent molecular evidence has placed *Hemigrapsus* species within the Varunidae, but this is currently debated and some authors still refer to them as members of the Grapsidae *sensu lato* (Ng et al. 2008; Wicksten 2011) and others have adopted the new familial designation (e.g. Kuris et al. 2007). Besides the higher taxonomic classifications, the known specific synonym for *H. nudus* is *Pseudograpsus nudus* (Wicksten 2011), which is not currently used.

Description

Size: Carapace 56.2 mm in width and 48 mm in length (Rathbun 1918; Wicksten 2011) (Fig. 1). An adult male from Coos Bay, was 32 mm in width and weighed 17.5 g (wet weight).

Color: Red, purple, or whitish with chelipeds that are red-spotted (compare to *H. oregonensis*, Plate 21 Kozloff 1993; Kuris et al. 2007) (Fig. 1). Although coloration is generally species-specific among grapsid crabs, nearly white or yellow forms of both *Hemigrapsus* species have been reported (Wicksten 2011).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are reduced and folded ventrally (Decapoda, Kuris et al. 2007).

Cephalothorax:

Eyes: Eystalks and eyes of moderate size with eyes that are at antero-

lateral angles (Fig. 2). Grapsid species apparently have keen vision (Wicksten 2011).

Antennae:

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004).

Carapace: Flat, smooth, punctate (Schmitt 1921) and bears three teeth (two lateral that are posterior to postorbital) (Wicksten 2011). Square in shape, with rounded antero-lateral margins (Rathbun 1918) and no transverse lines (compare to *P. crassipes*) (Fig. 1). Posteriorly, carapace is flat (Wicksten 2011) (Fig. 1).

Frontal Area: Very slightly rounded and without prominent lobes (Fig. 2).

Teeth: Two carapace teeth below the orbital tooth, which are lateral, while the last tooth is small (Fig. 2) (Wicksten 2011).

Pereopods: Naked (without hair) and rather short (Schmitt 1921) with short dactyls (Fig. 1) (Wicksten 2011).

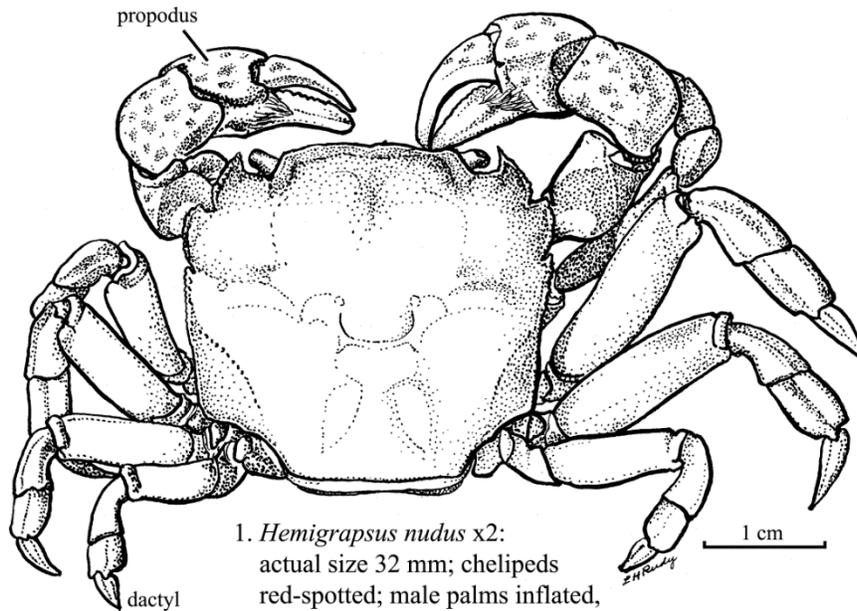
Chelipeds: Smooth, equal or almost equal in size with curved fingers (Wicksten 2011). Chelipeds stout, mottled above, with teeth on margins and with small round red spots (Fig. 1). Male with inflated palms and a patch of fine hair on inner surface.

Abdomen (Pleon): Females with wide abdomen and male *H. nudus* have narrow abdomens that exposes the sternum at the base (see **Sexual Dimorphism**, Fig. 3).

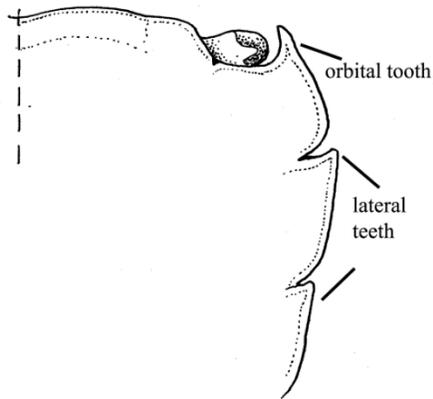
Telson & Uropods:

Sexual Dimorphism: Male and female brachyuran crabs are easily differentiable. The most conspicuous feature, the abdomen, is narrow and triangular in males while it is wide and flap-like in females (Brachyura, Kuris et al. 2007). Male *H. nudus* have a narrow abdomen, exposing the sternum at the base (Fig. 3) and the palm of the male cheliped with a patch of long, fine hair. Females have a wide abdomen, hiding the

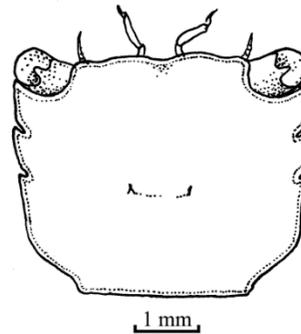
Hemigrapsus nudus



1. *Hemigrapsus nudus* x2:
actual size 32 mm; chelipeds
red-spotted; male palms inflated,
hairy; carapace flat, quadrate;
legs hairless; frontal area
slightly rounded.



2. Carapace (right frontal):
eyes moderate, at antero-lateral
angle; two lateral teeth (one small).



3. Juvenile x10:
actual size 5 mm; shallow
frontal depression; slight
lateral spines; eyes large.

sternum (Fig. 3), and only a few isolated bristles on the palm of the cheliped.

Possible Misidentifications

Hemigrapsus species were formally members of the Grapsidae, a family characterized by the carpus of the third maxilliped not articulating near the anterior merus angle and by lateral mouth margins that are parallel or convergent (Wicksten 2011). The genus *Hemigrapsus* may now a member of the family Varunidae (see **Taxonomy**)

characterized by chelae morphology, gaping third maxillipeds and setose walking legs (Ng et al. 2008). Two *Hemigrapsus* species occur locally, *H. oregonensis* and *H. nudus*.

Hemigrapsus nudus, the purple shore crab, is larger than *H. oregonensis*, is “naked” (i.e. not hairy) on its walking legs and has chelipeds with conspicuous red spots. *Hemigrapsus nudus* lives mostly on the rocky open coast, but is also found in salt marshes (Knudsen 1964). *Hemigrapsus oregonensis* has been called a small, bleached edition of *H. nudus* (Ricketts and Calvin 1971). The following features are particularly useful in differentiating the two *Hemigrapsus* species: 1) *H. oregonensis* has a marked frontal notch where *H. nudus* has a shallow depression, 2) the lateral spines of *H. oregonensis* are sharp and distinctly separated from the side but *H. nudus* spines are not, 3) The dactyls of walking legs 1–3 are long in *H. oregonensis* and short in *H. nudus* and 4) the dactyl of the fourth walking leg is round in *H. oregonensis* and flat in *H. nudus* (Kuris et al. 2007). The final varunid crab that occurs locally is the introduced Chinese mitten crab, *Eriocheir sinensis*, but this species is very large and easily differentiable from either *Hemigrapsus* species.

Pachygrapsus crassipes, a consistent member of the Grapsidae, is a dark green crab with many transverse dark red striations on its legs and carapace (*H. oregonensis* is smooth), its frontal margin is straight and it has one lateral tooth, not two (Symons 1964). The only other, locally occurring grapsid crab, *Planes cyaneus*, is a pelagic species that is only found washed ashore on drift logs with gooseneck barnacles (Kuris et al. 2007).

Rhithropanopeus harrisi, an introduced xanthid (Panopeidae) mud crab, is sometimes found with *H. oregonensis* and potentially *H. nudus*. It has a slightly convergent sides,

strong dorsal ridges on its carapace and three sharp carapace teeth.

Ecological Information

Range: Type locality is Puget Sound, Washington (Ricketts and Calvin 1971). Known range includes Sitka, Alaska, to Gulf of California (Rathbun 1918). Uncommon in Southern California (Garth and Abbott 1980; Jaffe et al. 1987; Wicksten 2011).

Local Distribution: Coos, Siletz, and Tillamook Bay estuaries (and probably more Oregon estuaries) in rocky, brackish habitats.

Habitat: Semi-protected and protected rocky coasts and bays. Prefers coarse sand to gravel substrates overlain with large rock cover (Schmitt 1921; Kuris et al. 2007). In salt marshes, but not as commonly encountered as *H. oregonensis*, and in burrows and under driftwood. Less common in California salt marshes (Kozloff 1993).

Hemigrapsus nudus is common in mid tide pool regions (Ricketts and Calvin 1971) and is found in areas of swift water and large boulders (Puget Sound, Knudsen 1964).

Hemigrapsus nudus can be found in more exposed situations than *H. oregonensis* and withstands desiccation better (large specimens). The two *Hemigrapsus* species do co-occur, but one usually finds one or the other (Kozloff 1993).

Salinity: Occurs in outer shore full strength seawater, brackish and hyper-saline (estuarine marsh) waters. Can endure low salinities better at high temperatures (Todd and Dehnel 1960).

Temperature: *Hemigrapsus nudus* individuals can tolerate temperatures up to 33.6°C but are more tolerant of cold than warm temperatures and modify their behavior to regulate body temperature (McGaw 2003). Survival is most poor with low temperature combined with low salinity, but smallest specimens are most resistant to temperature extremes (Todd and Dehnel 1960).

Tidal Level: Strictly littoral (Ricketts and Calvin 1971) and found higher than *H. oregonensis*, but both species are found from high to low levels (Todd and Dehnel 1960). Occurs in the rockweed belt, underneath rocks and is commonly found just below high-tide level (Monterey, California, Hiatt 1948).

Hemigrapsus nudus is often found with *Pachygrapsus*, which extends higher into the intertidal and prefers larger rocks.

Associates: Territory overlaps with *Pachygrapsus crassipes* over whom it is dominant (Hiatt 1948) and occasionally with *H. oregonensis*. Parasitic castrating isopod, *Portunion conformis*, occurs in perivisceral cavity of some individuals (Garth and Abbott 1980). Can be host to nemertean *Carcinonemertes epialti*. *Hemigrapsus nudus*, *H. oregonensis* and *P. crassipes* can all be host to this nemertean egg predator, which can negatively impact brood mortality in these species (Shields and Kuris 1988). These three species can also serve as intermediate hosts for a variety of parasites including trematode metacercariae, larval trypanorhynch tapeworms, as well as *Polymorphus* acanthocephalan and nematode (*Ascarophis*) larvae (Kuris et al. 2007).
Abundance: Locally abundant (Ricketts and Calvin 1971) and less common south (e.g. Morrow Bay, California, Kuris et al. 2007).

Life-History Information

Reproduction: In Puget Sound, Washington, mating occurs between December and January and is similar to *Pachygrapsus* (Hiatt 1948; see Fig. 2, 3, Knudsen 1964), however *P. crassipes* exhibits peak breeding in summer months compared to winter months in *H. nudus* (Booolootian et al. 1959). Females ovigerous January through April, 70% ovigerous in late January and 99% with fertilized eggs early April. Hatching occurs between May and June (Puget Sound, Washington). This timeline can be earlier (hatching Oct–May in Monterey Bay, California) or later (ovigerous April–May, British Columbia, Canada and hatching July, Friday Harbor, Washington) (Jaffe et al. 1987; Puls 2001) depending on water temperature. Each brood contains 400–36,000 embryos and the production of second brood is rare. Embryos are approximately 380 µm in diameter and become 450 µm upon hatching (Jaffe et al. 1987). The reproduction and life-cycle of *C. epialti* is dependent on and corresponds to that of its host species. However, this nemertean is not host specific (unlike *Carcinonemertes errans* on *Cancer magister*) and occurs amongst egg masses of other species including *Hemigrapsus oregonensis*, *Pachygrapsus crassipes* (Kuris 1993; Roe et al. 2007; Kuris et al. 2007).
Larva: Larval development in *H. nudus* proceeds via a series of zoea (five total) and

megalopa stages, each marked by a molt. The zoea are planktotrophic and have large compound eyes and four spines: one each dorsal and rostral and two lateral (see Fig. 32, Puls 2001; Fig. 54.5, Martin 2014). The rostrum and dorsal spines are of equal length and the two lateral spines are shorter (Puls 2001). The first zoea has exospines on the telson, is approximately 1.2 mm (measured from tip of rostrum to tip of telson) and has lateral knobs on the second and third segments, where *H. oregonensis* has lateral knobs on only the second segment (Puls 2001). The larvae of *H. nudus* are also a bit larger and more robust than those of closely related *H. oregonensis* (Jaffe et al. 1987). The zoea of *Hemigrapsus* species and *P. crassipes* can be differentiated by body and eye size (Schlotterbeck 1976). *Hemigrapsus nudus* megalopae are rectangular and can be recognized by a posterior telson with setae (other than uropod setae) and a carapace that is 1.8 mm in length and 1.5 mm in width (Puls 2001).

Juvenile: A shallow depression is present along the frontal area, notches and lateral spines are not terribly sharp or clearly separated from the side. Eyes are large (Fig. 3) and dactyls are short with the dactyl of leg four quite flat (Carlton and Kuris 1975). Juveniles of both sexes with narrow abdomens.

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: An herbivore and detritivore that ingests algae infrequently (Kozloff 1993). Individuals forage in large numbers on the tops of rocks and stomach contents reveal amphipods and other crustaceans provide a small part of the diet (Knudsen 1964).

Predators: Fish, raccoons and probably blue herons. Also predated by *Pachygrapsus* (on newly molted animals).

Behavior: Although shore crabs are generally believed to be fast moving (Wicksten 2011), *H. nudus* is rather sluggish

and sometimes feigns death when disturbed (Hiatt 1948; Kuris et al. 2007). *Hemigrapsus nudus* is a nocturnal feeder (Garth and Abbott 1980) and males are more aggressive than females, fighting when attacked. Females, on the other hand, autotomize easily in order to escape (Knudsen 1964).

Bibliography

1. BOOLOOTIAN, R. A., A. C. GIESE, A. FARMANFAMAIAN, AND J. TUCKER. 1959. Reproductive cycles of five west coast crabs. *Physiological Zoology*. 32:213-220.
2. CARLTON, J. T., AND A. M. KURIS. 1975. Keys to decapod crustacea, p. 385-412. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
3. DE GRAVE, S., N. D. PENTCHEFF, S. T. AHYONG, T. CHAN, K. A. CRANDALL, P. C. DWORSCHAK, D. L. FELDER, R. M. FELDMANN, C. FRANSEN, L. Y. D. GOULDING, R. LEMAITRE, M. E. Y. LOW, J. W. MARTIN, P. K. L. NG, C. E. SCHWEITZER, S. H. TAN, D. TSHUDY, AND R. WETZER. 2009. A classification of living and fossil genera of decapod crustaceans. *Raffles Bulletin of Zoology*:1-109.
4. GARTH, J. S., AND D. P. ABBOTT. 1980. Brachyura: The true crabs, p. 594-630. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
5. HIATT, R. W. 1948. The biology of the lined shore crab *Pachygrapsus crassipes* Randall. *Pacific Science*. 2:135-213.
6. KNUDSEN, J. W. 1964. Observations of the reproductive cycles and ecology of the common Brachyura and crablike Anomura of Puget Sound, Washington. *Pacific Science*. 18:3-33.
7. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
8. KURIS, A. M. 1993. Life cycles of nemertean predators of decapod crustacea: adaptations to host life histories. *Hydrobiologia*. 266:1-14.
9. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, AND E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
10. MARTIN, J. W. 2014. Brachyura, p. 295-310. *In: Atlas of crustacean larvae*. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
11. MCGAW, I. J. 2003. Behavioral thermoregulation in *Hemigrapsus nudus*, the amphibious purple shore crab. *Biological Bulletin*. 204:38-49.
12. NG, P. K. L., D. GUINOT, AND P. J. F. DAVIE. 2008. Systema brachyurorum: Part I. Annotated checklist of the extant Brachyuran crabs of the world. *Raffles Bulletin of Zoology Supplement*. 17:1-286.
13. NYBLADE, C. F. 1987. Phylum or Subphylum Crustacea, Class Malacostraca, Order Decapoda, Anomura, p. 441-450. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
14. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification Guide to Larval Marine Invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
15. RATHBUN, M. J. 1918. The grapsoid crabs of America. *Bulletin of the United States Natural Museum*. 97:128-145.
16. RICKETTS, E. F., AND J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
17. ROE, P., J. L. NORENBURG, AND S. MASLAKOVA. 2007. Nemertea, p. 221-233. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton

- (ed.). University of California Press, Berkeley, CA.
18. RUPPERT, E. E., R. S. FOX, AND R. D. BARNES. 2004. Invertebrate zoology: a functional evolutionary approach. Thomson Brooks/Cole, Belmont, CA.
 19. SCHLOTTERBECK, R. E. 1976. Larval development of the lined shore crab, *Pachygrapsus crassipes* Randall, 1840. (Decapod: Brachyura: Grapsidae) reared in the laboratory. *Crustaceana*. 30:184-200.
 20. SCHMITT, W. L. 1921. The marine decapod crustacea of California. University of California Publications in Zoology. 23:1-470.
 21. SCHUBART, C. D. 2011. Reconstruction of phylogenetic relationships within Grapsidae (Crustacea: Brachyura) and comparison of trans-isthmian versus amphi-atlantic gene flow based on mtDNA. *Zoologischer Anzeiger*. 250:472-478.
 22. SCHUBART, C. D., J. A. CUESTA, R. DIESEL, AND D. L. FELDER. 2000. Molecular phylogeny, taxonomy, and evolution of non-marine lineages within the American grapsoid crabs (Crustacea: Brachyura). *Molecular Phylogenetics and Evolution*. 15:179-190.
 23. SHIELDS, J. D., AND A. M. KURIS. 1988. Temporal variation in abundance of the egg predator *Carcinonemertes epialti* (Nemertea) and its effect on egg mortality of its host, the shore crab, *Hemigrapsus oregonensis*. *Hydrobiologia*. 156:31-38.
 24. SYMONS, P. E. K. 1964. Behavioral responses of the crab *Hemigrapsus oregonensis* to temperature, diurnal light variation, and food stimuli. *Ecology*. 45:580-591.
 25. TODD, M.-E., AND P. A. DEHNEL. 1960. Effect of temperature and salinity on heat tolerance in two grapsoid crabs, *Hemigrapsus nudus* and *Hemigrapsus oregonensis*. *Biological Bulletin*. 118:150-172.
 26. VON STERNBERG, R., AND N. CUMBERLIDGE. 1998. Taxic relationships within the Grapsidae MacLeay, 1838 (Crustacea: Decapoda: Eubrachyura). *Journal of Comparative Biology*. 3:115-136.
 27. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

Hemigrapsus oregonensis

A hairy shore crab

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Brachyura
Family: Varunidae

Taxonomy: The brachyuran family Grapsidae, the shore crabs, was a very large family with several subfamilies and little taxonomic scrutiny, until recently. Based on molecular and morphological evidence, authors (von Sternberg and Cumberlidge 2000; Schubart et al. 2000; de Grave et al. 2009; Schubart 2011) elevated all grapsid subfamilies to family level, reducing the number of species formally within the Grapsidae. Recent molecular evidence has placed *Hemigrapsus* species within the Varunidae, but this is currently debated where some authors still refer to them as members of the Grapsidae *sensu lato* (Ng et al. 2008; Wicksten 2012) and others have adopted the new familial designation (e.g. Kuris et al. 2007). Besides the higher taxonomic classifications, the known specific synonym for *H. oregonensis* is *Pseudograpsus oregonensis* (Wicksten 2012), which is not currently used.

Description

Size: Carapace 34.7 mm in width and 28.4 mm in length (Rathbun 1918; Wicksten 2012) (Fig. 1). The carapace of reproductive individuals measures approximately 50 mm (Puls 2001).

Color: Dull brownish green, gray to uniform light gray or muddy yellow with no red spots on chelipeds (compare *H. nudus*, Plate 21, Kozloff 1993; Kuris et al. 2007). Nearly white or yellow forms of both *Hemigrapsus* species have been reported (Ricketts and Calvin 1971; Wicksten 2012).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The abdomen and associated appendages are reduced and folded ventrally (Decapoda, Kuris et al. 2007).

Cephalothorax:

Eyes: Eyestalks and orbits moderately sized (Rathbun 1918) and eyes at antero-lateral angle (Fig. 2).

Antennae:

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004).

Carapace: Rectangular or square in shape and wider than long with rounded antero-lateral margins. Carapace surface is smooth and bears three teeth (two lateral that are posterior to postorbital) (Wicksten 2012) on antero-lateral margin, no transverse lines (Fig. 1).

Frontal Area: Less than half the width of the carapace with two prominent frontal lobes and deep median sinus (Wicksten 2012). Frontal margin without teeth (*Hemigrapsus*, Kuris et al. 2007).

Teeth: Two lateral carapace teeth, with deep sinuses, below outer orbital tooth (Fig. 2).

Pereopods: More or less hairy (compare to *H. nudus*) (Fig. 1).

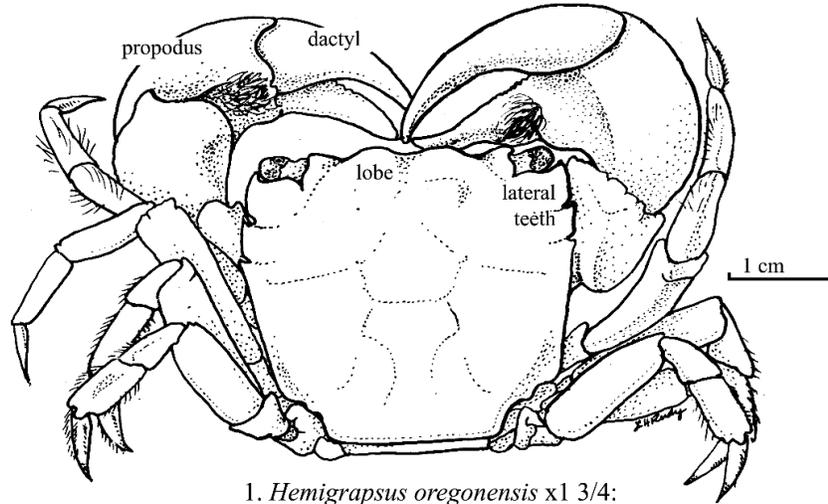
Chelipeds: Stout and equal or almost equal in size. Dactyls hollowed in shallow groove and male with mat of fine hair on propodus.

Abdomen (Pleon): Females with wide abdomen and male *H. oregonensis* have narrow abdomens that exposes the sternum at the base (see **Sexual Dimorphism**, Fig. 3).

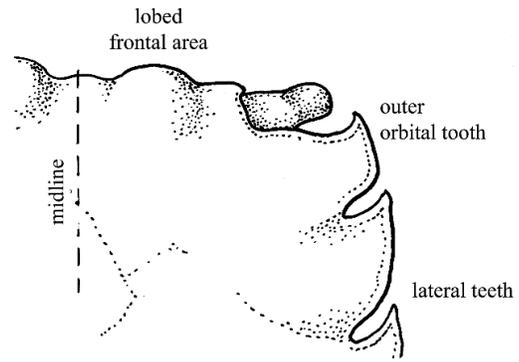
Telson & Uropods:

Sexual Dimorphism: Male and female brachyuran crabs are easily differentiable. The most conspicuous feature, the abdomen, is narrow and triangular in males while it is wide and flap-like in females (Brachyura, Kuris et al. 2007). Male *H. oregonensis* have a narrow abdomen that exposes the sternum (Fig. 3) and hairy chelipeds. Females have a wide abdomen and ho hairy patch on palm (only a few bristles).

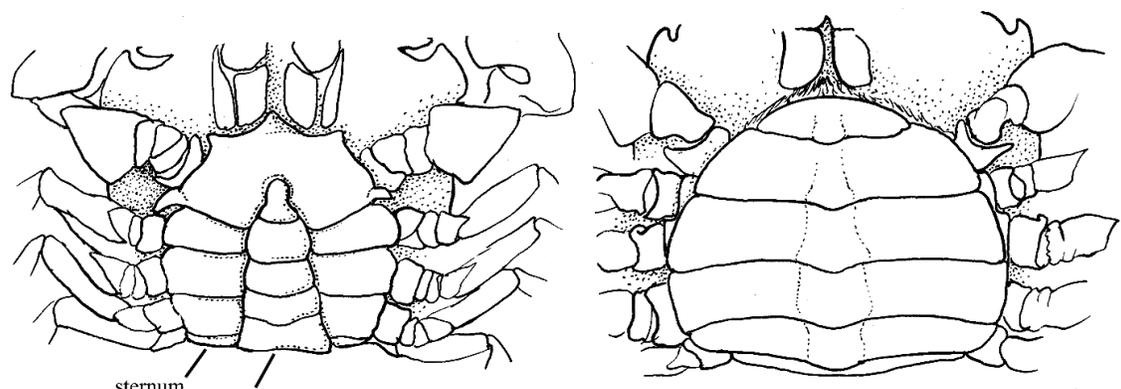
Hemigrapsus oregonensis



1. *Hemigrapsus oregonensis* x1 3/4:
actual size 32 mm; patch of fine hair
on male chela; legs hairy; carapace
quadrate, smooth; frontal area: two lobes.



2. Carapace (right frontal):
eyes moderate, at antero-lateral
angles; two deep lateral teeth.



3. Carapace (ventral view)

a. Male:
abdomen narrow, sternum visible at sides.

b. Female:
abdomen wide, sternum not visible.

Possible Misidentifications

Hemigrapsus species were formally members of the Grapsidae, a family characterized by the carpus of the third maxilliped not articulating near the anterior merus angle and by lateral mouth margins that are parallel or convergent (Wicksten 2012). The genus *Hemigrapsus* may now be a member of the family Varunidae (see **Taxonomy**) characterized by chelae morphology, gaping third maxillipeds and setose walking legs (Ng et al. 2008). Two *Hemigrapsus* species occur locally, *H. oregonensis* and *H. nudus*. *Hemigrapsus nudus*, the purple shore crab, is larger than *H. oregonensis*, is “naked” (i.e. not hairy) on its walking legs and has chelipeds with conspicuous red spots. *Hemigrapsus nudus* lives mostly on the rocky open coast, but is also found in salt marshes (Knudsen 1964). *Hemigrapsus oregonensis* has been called a small, bleached edition of *H. nudus* (Ricketts and Calvin 1971). The following features are particularly useful in differentiating the two *Hemigrapsus* species: 1) *H. oregonensis* has a marked frontal notch where *H. nudus* has a shallow depression, 2) the lateral spines of *H. oregonensis* are sharp and distinctly separated from the side but *H. nudus* spines are not, 3) The dactyls of walking legs 1–3 are long in *H. oregonensis* and short in *H. nudus* and 4) the dactyl of the fourth walking leg is round in *H. oregonensis* and flat in *H. nudus* (Kuris et al. 2007). The final varunid crab that occurs locally is the introduced Chinese mitten crab, *Eriocheir sinensis*, but this species is very large and easily differentiable from either *Hemigrapsus* species.

Pachygrapsus crassipes, a member of the Grapsidae, is a dark green crab with many transverse dark red striations on its legs and carapace (*H. oregonensis* is smooth), its frontal margin is straight and it has one lateral tooth, not two (Symons 1964). The only other locally occurring grapsid crab, *Planes cyaneus*, is a pelagic species that is only found washed ashore on drift logs with gooseneck barnacles (Kuris et al. 2007). *Rhithropanopeus harrisi*, an introduced xanthid (Panopeidae) mud crab, is sometimes found with *H. oregonensis*. It has a slightly convergent sides, strong dorsal ridges on its carapace and three sharp carapace teeth.

Ecological Information

Range: Type locality is Puget Sound, Washington. Known range includes Alaska to Baja California, Mexico (Wicksten 2012).

Local Distribution: Common in many Oregon bays including Yaquina, Siletz, Tillamook, Netarts, Coos and Coquille (Ricketts and Calvin 1971).

Habitat: Quiet water, rocky habitats within estuaries, gravel shores but prefers muddy habitats (Ricketts and Calvin 1971) and salt marshes. On muddy bottoms of estuaries and on eelgrass and amongst *Enteromorpha*. Also in muddy spots on the open rocky coast. The two *Hemigrapsus* species can co-occur, but one usually finds one or the other and *H. oregonensis* prefers quieter water than does *H. nudus* (Kozloff 1993).

Salinity: *Hemigrapsus oregonensis* tolerates salinity ranging from 17.5–31.6 (San Francisco, California), likes freshwater seeps (Garth and Abbott 1980) and cannot tolerate much desiccation.

Temperature: Small animals most tolerant to temperature extremes (Todd and Dehnel 1960).

Tidal Level: Found at very high and very low tide levels, but usually lower intertidal than *H. nudus* (Todd and Dehnel 1960). Individuals can be found at higher tidal reaches of the mudflats (Ricketts and Calvin 1971) and mid to low intertidal of bays as well as sublittorally (Kuris et al. 2007).

Associates: *Hemigrapsus oregonensis* has many associates. In gravel, isopods *Idotea* and *Gnorimosphaeroma*, and occasionally *H. nudus* (Kozloff 1993). Alga *Ulva* (sublittorally), and pickleweed, *Salicornia* (in marshes) (Kuris et al. 2007; Wicksten 2012). The parasitic castrating isopod, *Portunio conformis*, is sometimes within the perivisceral cavity of *H. oregonensis* (Garth and Abbott 1980) with infection rates up to 40% (Jaffe et al. 1987; Kuris et al. 2007). *Hemigrapsus oregonensis*, *H. nudus* and *P. crassipes* can all be host to the nemertean egg predator, *Carcinonemertes epialti*, which can negatively impact brood mortality in these species (Shields and Kuris 1988). These three species can also serve as intermediate hosts for a variety of parasites including trematode metacercariae, larval trypanorhynch tapeworms, as well as *Polymorphus* acanthocephalan and nematode (*Ascarophis*) larvae (Kuris et al. 2007).

Abundance: In great numbers, benthically, in estuaries and usually common on gravelly substrates (Wicksten 2012).

Life-History Information

Reproduction: In Vancouver, Canada, females are ovigerous in March and hatch in May, while in Puget Sound, Washington, they are ovigerous earlier (in Feb–April) and hatch between May and July. Broods include 800–11,000 embryos and 70% of females produce a second brood that will hatch in September. Embryos change color as they mature from white to purple to brown before they hatch at which time they are approximately 300–400 µm in diameter (Jaffe et al. 1987). In the lab, hatching occurs after 44 days (10–12°C, Jaffe et al. 1987). The reproduction and life-cycle of *C. epialti* is dependent on and corresponds to that of its host species. However, this nemertean is not host specific (unlike *Carcinonemertes errans* on *Cancer magister*) and occurs amongst egg masses of other species including *H. nudus*, *Pachygrapsus crassipes* (Roe et al. 2007). Interestingly, it may be more common on *H. oregonensis* than *P. producta*, for which it was described (Kuris 1993; Kuris et al. 2007).

Larva: Larval development in *H. oregonensis* proceeds via a series of zoea (five total) and megalopae stages, each marked by a molt. The zoea are planktotrophic and have large compound eyes and four spines: one each dorsal and rostral and two lateral (see Fig. 32, Puls 2001; Fig. 54.5, Martin 2014). The rostrum and dorsal spines are of equal length and the two lateral spines are shorter (Puls 2001). The first zoea has exospines on the telson, is approximately 1.1 mm (measured from tip of rostrum to tip of telson) and has lateral knobs on the second segment only, where *H. nudus* has lateral knobs on the second and third segments (Puls 2001). The larvae of *H. oregonensis* are also a bit smaller and more slender than that of the closely related *H. nudus* (Jaffe et al. 1987). The zoea of *Hemigrapsus* species and *P. crassipes* can be differentiated by body and eye size (Schlotterbeck 1976). *Hemigrapsus oregonensis* megalopae are rectangular and can be recognized by a posterior telson without setae (other than uropod setae) and a carapace that is 1.4–1.7 mm in length and 1.1–1.3 mm in width. The first in-star stage is

reached after approximately 4–5 weeks (Puls 2001).

Juvenile: Very small animals have a marked frontal notch and sharp lateral spines and long dactyls on walking legs (1–3) (Smith and Carlton 1975). Juveniles in both sexes have narrow abdomens.

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: Primarily an herbivore, scraping *Ulva* or *Enteromorpha* off rocks, *H. oregonensis* uses tactile, visual and chemical sense to find food (Knudsen 1964; Kozloff 1993).

Predators: Birds (e.g. willet, Rathbun 1918).

Behavior: A moderately active species that is a good digger and probably nocturnal (Knudsen 1964; Garth and Abbott 1980; Kuris et al. 2007).

Bibliography

1. DE GRAVE, S., N. D. PENTCHEFF, S. T. AHYONG, T. CHAN, K. A. CRANDALL, P. C. DWORSCHAK, D. L. FELDER, R. M. FELDMANN, C. FRANSEN, L. Y. D. GOULDING, R. LEMAITRE, M. E. Y. LOW, J. W. MARTIN, P. K. L. NG, C. E. SCHWEITZER, S. H. TAN, D. TSHUDY, and R. WETZER. 2009. A classification of living and fossil genera of decapod crustaceans. *Raffles Bulletin of Zoology*:1-109.
2. GARTH, J. S., and D. P. ABBOTT. 1980. Brachyura: The true crabs, p. 594-630. *In*: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
3. KNUDSEN, J. W. 1964. Observations of the reproductive cycles and ecology of the common Brachyura and crablike Anomura of Puget Sound, Washington. *Pacific Science*. 18:3-33.

4. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated Guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
5. KURIS, A. M. 1993. Life cycles of nemerteans that are symbiotic egg predators of decapod crustacea: adaptations to host life histories. *Hydrobiologia*. 266:1-14.
6. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
7. MARTIN, J. W. 2014. Brachyura, p. 295-310. *In: Atlas of crustacean larvae*. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
8. NG, P. K. L., D. GUINOT, and P. J. F. DAVIE. 2008. Systema brachyurorum: Part I. Annotated checklist of the extant Brachyuran crabs of the world. *Raffles Bulletin of Zoology Supplement*. 17:1-286.
9. NYBLADE, C. F. 1987. Phylum or Subphylum Crustacea, Class Malacostraca, Order Decapoda, Anomura, p. 441-450. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
10. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
11. RATHBUN, M. J. 1918. The grapsoid crabs of America. *Bulletin of the United States Natural Museum*. 97:128-145.
12. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
13. ROE, P., J. L. NORENBURG, and S. MASLAKOVA. 2007. Nemertea, p. 221-233. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
14. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*. Thomson Brooks/Cole, Belmont, CA.
15. SCHLOTTERBECK, R. E. 1976. Larval development of the lined shore crab, *Pachygrapsus crassipes* Randall, 1840. (Decapod: Brachyura: Grapsidae) reared in the laboratory. *Crustaceana*. 30:184-200.
16. SCHUBART, C. D. 2011. Reconstruction of phylogenetic relationships within Grapsidae (Crustacea: Brachyura) and comparison of trans-isthmian versus amphi-atlantic gene flow based on mtDNA. *Zoologischer Anzeiger*. 250:472-478.
17. SCHUBART, C. D., J. A. CUESTA, R. DIESEL, and D. L. FELDER. 2000. Molecular phylogeny, taxonomy, and evolution of non-marine lineages within the American grapsoid crabs (Crustacea: Brachyura). *Molecular Phylogenetics and Evolution*. 15:179-190.
18. SHIELDS, J. D., and A. M. KURIS. 1988. Temporal variation in abundance of the egg predator *Carcinonemertes epialti* (Nemertea) and its effect on egg mortality of its host, the shore crab, *Hemigrapsus oregonensis*. *Hydrobiologia*. 156:31-38.
19. SMITH, R. I., and J. T. CARLTON. 1975. *Light's manual: intertidal invertebrates of the central California coast*. University of California Press, Berkeley.
20. SYMONS, P. E. K. 1964. Behavioral responses of the crab *Hemigrapsus oregonensis* to temperature, diurnal light variation, and food stimuli. *Ecology*. 45:580-591.
21. TODD, M., and P. A. DEHNEL. 1960. Effect of temperature and salinity on heat tolerance in two grapsoid crabs, *Hemigrapsus nudus* and *Hemigrapsus oregonensis*. *Biological Bulletin*. 118:150-172.

22. VON STERNBERG, R., and N. CUMBERLIDGE. 1998. Taxic relationships within the Grapsidae (MacLeay, 1838) (Crustacea: Decapoda: Eubrachyura). *Journal of Comparative Biology*. 3:115-136.
23. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

Crangon alaskensis

Alaskan bay shrimp, salt-and-pepper shrimp

Phylum: Arthropoda
Class: Crustacea, Malacostraca
Order: Decapoda
Tribe: Caridea
Family: Crangonidae

Taxonomy: Schmitt (1921) described many shrimp in the genus *Crago* (e.g. *Crago alaskensis*) and reserved the genus *Crangon* for the snapping shrimp (now in the genus *Alpheus*). In 1955–56, the International Commission on Zoological Nomenclature formally reserved the genus *Crangon* for the sand shrimps. The subgeneric name *C. alaskensis elongata* was used briefly based on Alaskan specimens bearing shorter rostrums (Rathbun 1902), but this was not corroborated with data from Butler (1980) and Wicksten (2011) and is not widely used (e.g. Kuris et al. 2007; Wicksten 2011).

Description

Size: Type specimen was 76 mm (Carlton and Kuris 1975) and a female specimen from South Slough (of Coos Bay) was 65 mm. Average length is 52 mm for males and 65 mm for females (Wicksten 2011).

Color: White, mottled with small black spots, giving gray appearance, hence the common name: the salt-and-pepper shrimp. Body color rather dull and is camouflaged with chromatophores (Wicksten 2011).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The body is laterally compressed and shrimp-like in the Caridea. The abdomen and associated appendages are outstretched and the abdomen usually has a sharp bend (Kuris et al. 2007).

Cephalothorax:

Eyes: Salmon in color, free and not covered by the carapace (*Crangon* and *Lissocrangon*).

Antennae: Antennal scale (scaphocerite) narrow, with spine longer than blade, and more than 2/3 carapace length with blade broad and rounded (Fig. 2) (Plate

319B, Kuris et al. 2007). Stylocerite (basal, lateral spine on antennule) almost as long as first antennule peduncle segment (Wicksten 2011). Antennae 2/3 body length (Kuris et al. 2007).

Mouthparts: The mouth of decapod crustaceans is comprised of six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004). Third maxilliped setose and with exopod in *C. alaskensis* and *C. franciscorum* (Wicksten 2011).

Carapace: Thin and smooth, with a single medial spine (compare to *Lissocrangon* with no gastric spines). Also lateral (Schmitt 1921), hepatic, branchiostegal and pterygostomial spines (Wicksten 2011).

Rostrum: Rostrum straight and upturned (*Crangon*, Kuris and Carlton 1977). Short, flattened, rounded (Fig. 2) and unornamented. Rostrum length reaching or exceeding the cornea of the eye (Wicksten 2011).

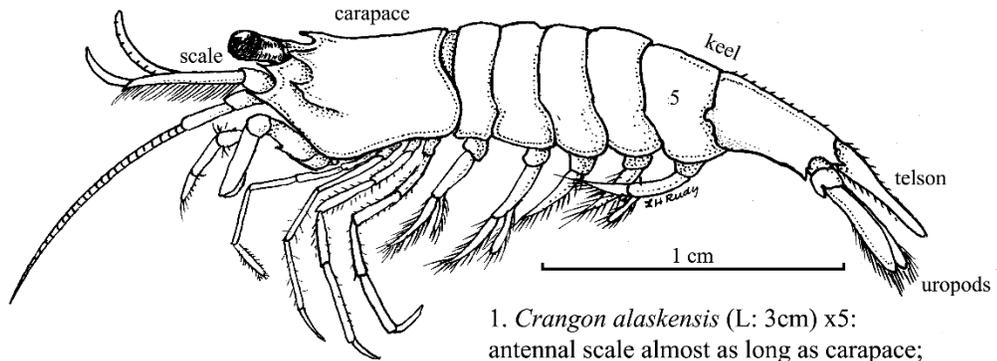
Teeth:

Pereopods: First pereopod subchelate, with inner spine. Merus with strong distal spine, broad propodus and dactyl that closes obliquely or horizontally across propodus (Wicksten 2011). Second to fifth pereopod morphology as follows: second pereopods slender, chelate and of equal size; third slender with simple dactyl; fourth and fifth longer than third and larger, also with simple dactyls.

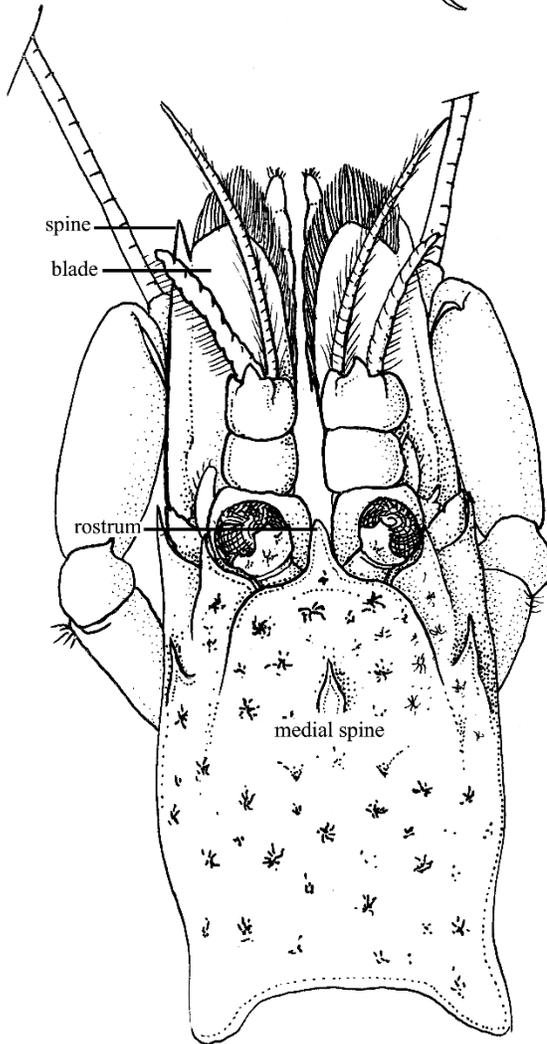
Chelipeds: Subchelate. Chela dactyl at a 45° angle to the hand (Plate 319A, Kuris et al. 2007) (Fig. 3).

Abdomen (Pleon): Shrimp-like, with typical caridean bend, the second segment overlaps the first (Fig. 1). Male abdomen narrow (see **Sexual Dimorphism**). Morphology of the sixth abdominal segment bears taxonomic significance. In *C. alaskensis*, it lacks dorsal carinae and the ventral side is sulcate and the

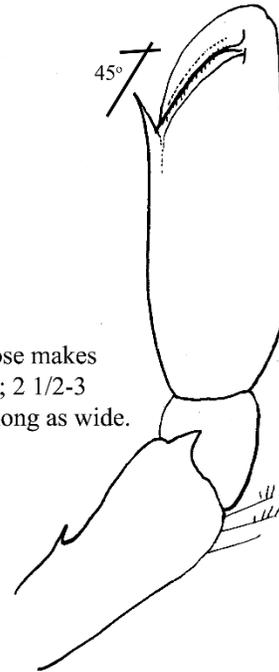
Crangon alaskensis



1. *Crangon alaskensis* (L: 3cm) x5:
antennal scale almost as long as carapace;
telson almost as long as uropods;
hands of first legs subchelate; eyes free.



2. Frontal region (dorsal view):
antennal spine larger than blade;
rostrum slender;
carapace: one medial spine.



3. Hand:
finger close makes
45° angle; 2 1/2-3
times as long as wide.

somite is with postero-lateral spine and ventral groove (Kuris and Carlton 1977; Wicksten 2011).

Telson & Uropods: Telson nearly equal to or longer in length than uropods (*Crangon*, Kuris and Carlton 1977). Telson has two pair dorso-lateral spines (Wicksten 2011).

Sexual Dimorphism: Females often have broader and larger bodies than males, which have compressed and squat bodies (Wicksten 2011).

Possible Misidentifications

The family Crangonidae is characterized by first pereopods that are subchelate and second pereopods (if present) that are slender and equal in size, each with unsegmented carpus. Other characters include chela dactyls that close horizontally across the end of the propodus ("like the blade of a pocket knife" Wicksten 2011), a rostrum that is small and without spines and a body that is squat and somewhat depressed (although it can be broad in ovigerous females) (Wicksten 2011).

Three crangonid genera were revised in 1977 by Kuris and Carlton: *Lissocrangon*, *Crangon* and *Neocrangon*. Members of the two former genera are found locally. These genera can be differentiated by carapace spination: *Lissocrangon* lacks gastric spines; *Crangon* has one median gastric spine; and *Neocrangon* (*Mesocrangon*, *M. munitella*, locally) has two gastric spines.

Besides lacking gastric spines, *Lissocrangon* species have a long narrow and sharply recurved rostrum, a telson that is shorter than the uropods and a sixth abdominal segment without a pair of dorsal carinae (keel-like ridges). This genus is monotypic, the only known member is *L. stylirostris* (Kuris and Carlton 1977; Kuris et al. 2007).

Crangon species have a straight and upturned rostrum and a telson that is of equal length or longer than uropods. The genus is divided into groups (i.e. subgenera, Kuris and Carlton 1977) based on characters of the sixth abdominal segment. In the first group, the sixth abdominal segment is smooth and lacks dorsal carinae (instead of two distal carinae). This group is further split based on a sulcate or convex sixth abdominal segment ventrum. The so-called "smooth, sulcate

species group" (Kuris and Carlton 1977) includes all local *Crangon* species, *C. alaskensis*, *C. franciscorum*, *C. handi*, *C. nigricauda* and *C. nigromaculata*.

Crangon nigricauda, the black tailed shrimp, has an antennal blade and spine of nearly equal length and cheliped fingers that close almost transversely. *Crangon nigromaculata* has a striking round marking on the side of the sixth abdominal segment, its fingers also close transversely, and its range may not extend north to Oregon. *Crangon handi*, from the outer coast, has a very short, stout antennal scale, and a short sixth abdominal segment (Kuris and Carlton 1977). *Crangon alaskensis* is a small shrimp, with a slender rostrum, and lacks *C. franciscorum*'s very long propodus. *Crangon alaskensis* can further be differentiated by the chela dactyl that is at a 45° angle to the hand (Plate 319A, Kuris et al. 2007) rather than nearly parallel as in *C. franciscorum*. Furthermore, *C. franciscorum* has a spine on the postero-dorsal corner of the fifth abdominal segment and the inner flagellum of the first antenna is more than two times as long as the outer (Plate 316A, Kuris et al. 2007). The rostrum length is variable in *C. alaskensis*, and Rathbun (1902) distinguished *C. alaskensis elongata* as a southern form, with longer rostrum than Alaskan forms (Wicksten 2011). However, data from specimens collected from British Columbia, Canada (Butler 1980) and San Diego, California (Wicksten 2011) dismissed any distinct latitudinal difference in morphology.

Ecological Information

Range: Type locality is Mutiny Bay, Alaska. Known range includes Bering Sea to Todos Santos Bay, Baja California (Wicksten 2011)

Local Distribution: Oregon estuaries and bays including Yaquina Bay (Rathbun 1902) and Coos Bay sites at Collver Point (South Slough) and the Charleston channel.

Habitat: Shallow water in bays and estuaries with soft, fine sand. Also in bay channel with muddy and rocky substrate.

Salinity: Euryhaline (Wicksten 2011). Collected at 30 (Rathbun 1902).

Temperature: Great toleration of temperature variation and prefers warmer water than *C. nigricauda*.

Tidal Level: Intertidal to 275 m (Wicksten 1984; Wicksten 2011).

Associates: Collected in a trawl with *Cancer jordani*, *Hermisenda* sp., *Rostanga pulchra*, and other sponges. Trematode metacercariae can also be found within the nervous system of *C. alaskensis* (Morado and Sparks 1983). Can be infested with Bopyrid isopod *Argeia pugettensis* (Butler 1980). This isopod is found next to the branchial chamber in many crangonids and forms a conspicuous bulge in the carapace (see Plate 19, Kozloff 1993; Wicksten 2011).

Abundance: Common and co-occurs with, the larger, *C. nigricauda*. Together, these species comprise the major decapod shrimp epifauna in Yaquina Bay, Oregon (Rathbun 1902).

Life-History Information

Reproduction: Many crangonid shrimp species are considered gonochoristic, but evidence suggests that some species exhibit protandry (Bauer 2004). Identifying ovigerous females is easy as female crangonid shrimp carry eggs, which are attached between the joints and rami of the inner pleopods under the abdomen (Siegfried 1989). Ovigerous females collected from May–August and October (Butler 1980; Nyblade 1987) and spawning reported from December to August (Yaquina Bay, Oregon, Rathbun 1902).

Larva: In caridean shrimp species, development proceeds through several zoea larval stages (Konishi and Kim 2000; Guerao and Cuesta 2014). Crangonid zoea are characterized by a wide rostrum, hemispherical eyestalks, antennule bases that touch, unsegmented antennule scales with inner flagellum having a setose spine, an exopod present on pereopod one (not 3–5), which is subchelate and a telson that widens posteriorly (see Fig. 48.1, Guerao and Cuesta 2014; Puls 2001).

Juvenile:

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the

ability to regenerate limbs that were previously autotomized (Kuris et al. 2007). Differential growth rate in *C. alaskensis* is large between females and males.

Food: Individuals feed on small invertebrates (Wicksten 2011).

Predators: Demersal fishes (e.g. *Hexagrammos decagrammus*, Nemeth 1997), Dungeness crabs and harbor seals (Wicksten 2011). Significant food source for young Striped Bass in upper Coos Bay (Rathbun 1902).

Behavior: Benthic shrimp that dig in the sand and remain hidden with only their eyes and antennae visible (Wicksten 2011).

Bibliography

1. BAUER, R. T. 2004. Remarkable shrimps: adaptations and natural history of the carideans. Animal Natural History Series. 7:1-282.
2. BUTLER, T. H. 1980. Shrimps of the Pacific coast of Canada. Canadian Bulletin of Fisheries and Aquatic Sciences:1-280.
3. CARLTON, J. T., and A. M. KURIS. 1975. Keys to Decapod crustacea, p. 385-412. *In*: Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
4. GUERAO, G., and J. A. CUESTA. 2014. Caridea, p. 250-255. *In*: Atlas of crustacean larvae. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
5. KONISHI, K., and J. N. KIM. 2000. The first zoeal stage of sand shrimp *Crangon amurensis* (Brashnikov, 1907), with a discussion of the larval characters of the Crangonidae (Crustacea, Decapoda, Caridea). Bulletin of National Research Institute of Aquaculture:1-12.
6. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
7. KURIS, A. M., and J. T. CARLTON. 1977. Description of a new species, *Crangon handi*, and new genus, *Lissocrangon*, of crangonid shrimps (Crustacea, Caridea) from California coast, with notes on adaptation in body shape and coloration. Biological Bulletin. 153:540-559.
8. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007.

- Decapoda, p. 632-656. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
9. MORADO, J. F., and A. K. SPARKS. 1983. Infection of nervous tissue of shrimp, *Crangon alaskensis*, by *Trematode metacercariae*. *Journal of Invertebrate Pathology*. 42:421-423.
 10. NEMETH, D. H. 1997. Modulation of attack behavior and its effect on feeding performance in a trophic generalist fish, *Hexagrammos decagrammus*. *Journal of Experimental Biology*. 200:2155-2164.
 11. NYBLADE, C. F. 1987. Phylum or Subphylum Crustacea, Class Malacostraca, Order Decapoda, Anomura, p. 441-450. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 12. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 13. RATHBUN, M. J. 1902. Descriptions of new decapod crustaceans from the west coast of North America. *Proceedings of the United States National Museum*. 24:885-905.
 14. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*. Thomson Brooks/Cole, Belmont, CA.
 15. SCHMITT, W. L. 1921. The marine decapod crustacea of California. *University of California Publications in Zoology*. 23:1-470.
 16. SIEGFRIED, C. A. 1989. Species profiles, life histories, and environmental requirements of coastal fishes and invertebrates Pacific southwest crangonid shrimp. U S Fish and Wildlife Service Biological Report. 82:i-vi, 1-18.
 17. WICKSTEN, M. K. 1984. Distribution of some common decapod crustaceans and a pycnogonid from the continental shelf of northern California. *California Fish and Game*. 70:132-139.
 18. —. 2011. Decapod Crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

Crangon franciscorum

Common gray shrimp

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Caridea
Family: Crangonidae

Taxonomy: Schmitt (1921) described many shrimp in the genus *Crago* (e.g. *Crago franciscorum*) and reserved the genus *Crangon* for the snapping shrimp (now in the genus *Alpheus*). In 1955–56, the International Commission on Zoological Nomenclature formally reserved the genus *Crangon* for the sand shrimps only. Recent taxonomic debate revolves around potential subgeneric designation for *C. franciscorum* (*C. Neocrangon franciscorum*, *C. franciscorum franciscorum*) (Christoffersen 1988; Kuris and Carlton 1977; Butler 1980; Wicksten 2011).

Description

Size: Average body length is 49 mm for males and 68 mm for females (Wicksten 2011).

Color: White, mottled with small black spots, giving gray appearance.

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The body is laterally compressed and shrimp-like in the Caridea. The abdomen and associated appendages are outstretched and the abdomen usually has a sharp bend (Kuris et al. 2007).

Cephalothorax:

Eyes: Eyes small, pigmented and not covered by carapace (Wicksten 2011).

Antennae: Antennal scale (scaphocerite) with spine longer than blade (Fig. 2). Stylocerite (basal, lateral spine on antennule) longer than first antennule peduncle segment (Wicksten 2011). Inner flagellum of the first antenna is greater than twice as long as the outer flagellum (Kuris et al. 2007) (Fig. 2).

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles

(on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004). Third maxilliped setose and with exopod in *C. franciscorum* and *C. alaskensis* (Wicksten 2011).

Carapace: Thin and smooth, with a single medial spine (compare to *Lissocrangon* with no gastric spines). Also lateral (Schmitt 1921) (Fig. 1), hepatic, branchiostegal and pterygostomial spines (Wicksten 2011).

Rostrum: Rostrum straight and upturned (*Crangon*, Kuris and Carlton 1977). Short, flattened, rounded (Fig. 2) and unornamented. Rostrum length reaching or exceeding the cornea of the eye (Wicksten 2011).

Teeth:

Pereopods: Inner spine on merus of first pereopod, hand of subchela elongate and dactyl closes longitudinally (versus obliquely) against inner spine. Second to fifth pereopod morphology as follows: second pereopod slender and chelate; third slender and with simple dactyl; fourth and fifth larger than third and bearing setae, also with simple dactyls (Wicksten 2011).

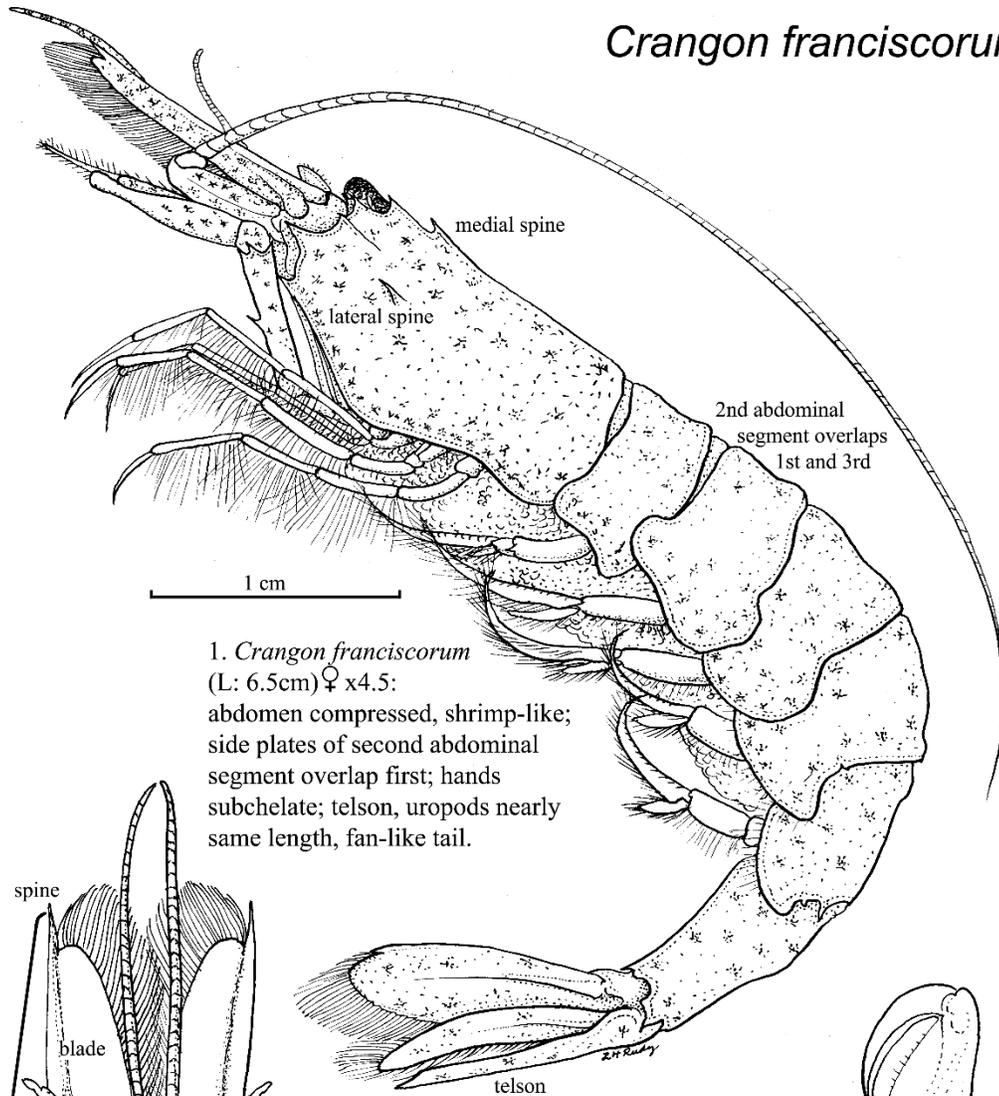
Chelipeds: Subchelate. Dactyl almost parallel to hand (Plate 319A, Kuris et al. 2007) (Fig. 3).

Abdomen (Pleon): Shrimp-like, with typical caridean bend, the second segment overlaps the first (Fig. 1). Male abdomen narrow (see **Sexual Dimorphism**). Bears rounded pleura and fifth segment with postero-lateral spine. Morphology of the sixth abdominal segment is taxonomically significant—in *C. franciscorum*, the sixth segment is slender, with postero-ventral spine and ventral groove (Wicksten 2011).

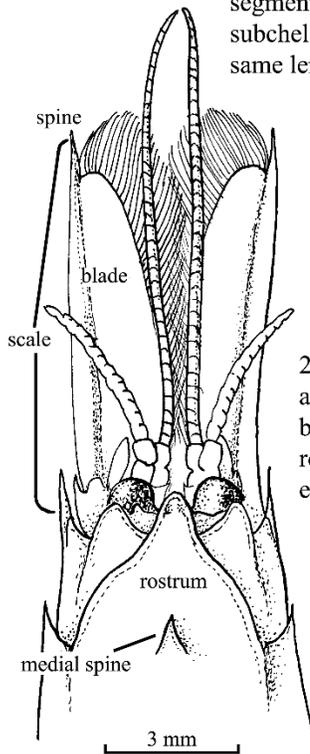
Telson & Uropods: Telson shorter than uropods. Telson is narrow and with two pairs of lateral spines, acute apex (Wicksten 2011).

Sexual Dimorphism: Females often have broader and larger bodies than males, which have compressed and squat bodies

Crangon franciscorum

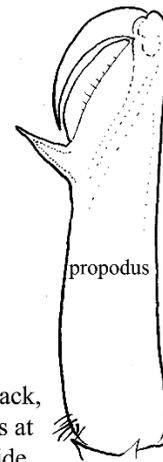


1. *Crangon franciscorum*
 (L: 6.5cm) ♀ x4.5:
 abdomen compressed, shrimp-like;
 side plates of second abdominal
 segment overlap first; hands
 subchelate; telson, uropods nearly
 same length, fan-like tail.



2. Head x8:
 antennal scale 3/4 length of carapace;
 blade broad, rounded; spine long;
 rostrum short, flattened; rounded;
 eyes free; carapace with medial spine.

3. First cheliped:
 hand slender, finger turned back,
 nearly longitudinal; propodus at
 least four times as long as wide.



(Wicksten 2011). See also variations in endopod morphology (Fig. 4, Siegfried 1989).

Possible Misidentifications

The family Crangonidae is characterized by first pereopods that are subchelate and second pereopods (if present) that are slender and equal in size, each with unsegmented carpus. Other characters include chela dactyls that close horizontally across the end of the propodus (“like the blade of a pocket knife” Wicksten 2011), a rostrum that is small and without spines and a body that is squat and somewhat depressed (although it can be broad in ovigerous females) (Wicksten 2011).

Three crangonid genera were revised in 1977 by Kuris and Carlton: *Lissocrangon*, *Crangon* and *Neocrangon*. Members of the two former genera are found locally. These genera can be differentiated by carapace spination: *Lissocrangon* lacks gastric spines; *Crangon* has one median gastric spine; and *Neocrangon* (*Mesocrangon*, *M. munitella*, locally) has two gastric spines.

Besides lacking gastric spines, *Lissocrangon* species have a long, narrow and sharply recurved rostrum, a telson that is shorter than the uropods and a sixth abdominal segment without a pair of dorsal carinae (keel-like ridges). This genus is monotypic, the only known member is *L. stylirostris* (Kuris and Carlton 1977; Kuris et al. 2007).

Crangon species have a straight and upturned rostrum and a telson that is of equal length or longer than uropods. The genus is divided into groups (i.e. subgenera, Kuris and Carlton 1977) based on characters of the sixth abdominal segment. In the first group, the sixth abdominal segment is smooth and lacks dorsal carinae (instead of two distal carinae). This group is further split based on a sulcate or convex sixth abdominal segment ventrum. The so-called “smooth, sulcate species group” (Kuris and Carlton 1977) includes all local *Crangon* species, *C. alaskensis*, *C. franciscorum*, *C. handi*, *C. nigricauda* and *C. nigromaculata*.

Crangon nigricauda, the black tailed shrimp, has an antennal blade and spine of nearly equal length and cheliped fingers that close almost transversely. *Crangon nigromaculata* has a striking round marking on the side of the sixth abdominal segment,

its fingers also close transversely, and its range may not extend north to Oregon.

Crangon handi, from the outer coast, has a very short, stout antennal scale, and a short sixth abdominal segment (Kuris and Carlton 1977). *Crangon alaskensis* is a small shrimp, with a slender rostrum, and lacks *C. franciscorum*'s very long propodus. *Crangon franciscorum* can further be differentiated from *C. alaskensis* by the chela dactyl that is almost parallel to the hand (Plate 319A, Kuris et al. 2007) rather than at a 45° angle. Furthermore, *C. franciscorum* has a spine on the postero-dorsal corner of the fifth abdominal segment and an inner flagellum of the first antenna that is more than two times as long as the outer (Plate 316A, Kuris et al. 2007). Butler calls this species *Crangon franciscorum franciscorum*, to distinguish it from *C.f. angustimana* Rathbun 1902, the long-clawed *Crangon* (Butler 1980). This latter species lives in deeper water, and within a narrower range of temperatures than does *C. f. franciscorum* (Butler 1980).

Ecological Information

Range: Type locality is San Francisco Bay, California. Known range includes Resurrection Bay, Alaska to San Diego, California (Schmitt 1921; Wicksten 2011).

Local Distribution: Yaquina Bay; South Slough (Collver Point, channel) (Krygiel and Horton 1975).

Habitat: Shallow water in bays and estuaries with soft substrate. In bay channel with muddy and rocky substrate, also offshore in deeper water (Kuris et al. 2007; Wicksten 2011).

Salinity: Euryhaline and collected at 30, with salinity range from 0.2–34.4 (Krygiel and Horton 1975; Wahle 1985; Wicksten 2011; Campos et al. 2012).

Temperature: Great toleration of temperature variation (e.g. 5–25°C, Campos et al. 2012) prefers warmer water than *C. nigricauda* (Krygiel and Horton 1975).

Tidal Level: Intertidal to 91 m (Schmitt 1921; Wicksten 2011).

Associates: Collected in a trawl with *Cancer jordani*, *Hermisenda* sp., *Rostanga pulchra*, and other sponges. Can be infested with Bopyrid isopod *Argeia pugettensis* (Butler 1980). This isopod is found next to the branchial chamber in many crangonids and forms a conspicuous bulge in the carapace

(see Plate 19, Kozloff 1993; Wicksten 2011). The crangonid shrimps *L. stylirostris* and *Crangon franciscorum* may also be infected with the microsporidium parasite *Pleistophora crangoni*, which occurs within their skeletal musculature (Breed and Olson 1977). *Crangon franciscorum* individuals can also be infected with chitinoclastic bacteria that causes bacterial shell disease (*Vibrio* spp. and *Pseudomonas* sp.). This type of bacterial infection causes the exoskeleton to be darkened, cracked and amorphous, with underlying tissue lesions (Arnold and Hendrickson 1997).

Abundance: Common to abundant (Kuris et al. 2007).

Life-History Information

Reproduction: Many crangonid shrimp species are considered gonochoristic, but evidence suggests that some species exhibit protandry (Bauer 2004). Identifying ovigerous females is easy as female crangonid shrimp carry eggs, which are attached with between the joints and rami of the inner pleopods, under the abdomen and spawning has been observed almost year-round (Siegfried 1989). Ovigerous females collected from Dec–May, June or August and hatching reported from early spring to summer (San Francisco Bay, California, Israel 1936; Yaquina Bay, Oregon, Krygier and Horton 1975; Strathmann 1987; Campos et al. 2012) during periods or in locations of high salinity (Israel 1936). A spawning migration was described by Krygier and Horton where ovigerous females moved to more haline and deeper water prior to spawning (1975). *Crangon franciscorum* exhibits protandric hermaphroditism where males and females can switch from one sex to another and associated morphological changes can be observed (e.g. shape of pleopod morphology) (Gavio et al. 1994; Gavio et al. 2006).

Larva: In caridean shrimp species development proceeds through several zoea larval stages (Konishi 2000; Guerao and Cuesta 2014). Crangonid zoea are characterized by a wide rostrum, hemispherical eyestalks, antennule bases that touch, unsegmented antennule scales with inner flagellum having a setose spine, an exopod present on pereopod one (not 3–5), which is subchelate and a telson that widens posteriorly (see Fig. 48.1, Guerao and Cuesta

2014; Puls 2001). Larval stages occur in the plankton and earliest post-larval shrimp found in brackish water of shallow tidal flats—mature animals move into deeper water (Israel 1936).

Juvenile:

Longevity: Females live a maximum 1 1/2 years and males up to one year (Krygier and Horton 1975; Gavio et al. 2006).

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007). Differential growth rate in *C. franciscorum* is large between females and males and juvenile growth ranged from 0.76–1.37 mm per week (Oregon, Krygier and Horton 1975).

Food: The diets of co-occurring crangonid species, *Crangon franciscorum* and *C. nigricauda*, have been described (Wahle 1985). Individuals feed on small invertebrates (e.g. *Neomysis mercedis*, Sitts and Knight 1979; amphipods, bivalves, Wahle 1985) and, in the Columbia River estuary *C. franciscorum* accounted for a high proportion of the total suspended particle consumption (Simenstad et al. 1990).

Predators: Demersal fishes, Dungeness crabs and harbor seals (Wicksten 2011). Commercially harvested in San Francisco Bay, California for bait with *L. stylirostris*, *C. nigricauda* and *C. nigromaculata* (Israel 1936). Annual catches ranged from 320,000–1,360,000 kg (1940–1957) to 2,300–25,000 kg (1980s) per year (Chace and Abbott 1980). **Behavior:** Benthic shrimp that dig in the sand and remain hidden with only their eyes and antennae visible (Wicksten 2011).

Bibliography

1. ARNOLD, J. D., and G. L. HENDRICKSON. 1997. Bacterial shell disease in crangonid shrimp. California Fish and Game. 83:118-127.
2. BAUER, R. T. 2004. Remarkable shrimps: adaptations and natural

- history of the carideans. *Animal Natural History Series*. 7:1-282.
3. BREED, G. M., and R. E. OLSON. 1977. Biology of microsporidan parasite *Pleistophora crangonin* n.sp. in three species of crangonid sand shrimps. *Journal of Invertebrate Pathology*. 30:387-405.
 4. BUTLER, T. H. 1980. Shrimps of the Pacific Coast of Canada. *Canadian Bulletin of Fish and Aquatic Sciences*. 202:1-280.
 5. CAMPOS, J., C. MOREIRA, F. FREITAS, and H. W. VAN DER VEER. 2012. Short review of the eco-geography of Crangon. *Journal of Crustacean Biology*. 32:159-169.
 6. CHACE, F. A., D. P. ABBOTT, R. H. MORRIS, and E. C. HADERLIE. 1980. Caridea: the shrimps. *In: Intertidal invertebrates of California*. Stanford University Press, Stanford, CA.
 7. CHRISTOFFERSEN, M. L. 1988. Genealogy and phylogenetic classification of the world Crangonidae (Crustacea, Caridea), with a new species and new records for the south western Atlantic. *Revista Nordestina de Biologia*. 6:43-59.
 8. GAVIO, M. A., J. M. ORENSANZ, and D. ARMSTRONG. 1994. Protandric hermaphroditism in the bay shrimp *Crangon franciscorum* (Decapoda, Caridea). *Journal of Shellfish Research*. 13:292-292.
 9. —. 2006. Evaluation of alternative life history hypotheses for the sand shrimp *Crangon franciscorum* (Decapoda, Caridea). *Journal of Crustacean Biology*. 26:295-307.
 10. GUERAO, G., and J. A. CUESTA. 2014. Caridea, p. 250-255. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
 11. ISRAEL, H. R. 1936. A contribution toward the life histories of two California shrimps, *Crago franciscorum* and *Crago nigricauda*. *California Department of Fish and Game Bulletin*. 46:1-28.
 12. KONISHI, K., and J. N. KIM. 2000. The first zoeal stage of sand shrimp *Crangon amurensis* (Brashnikov, 1907), with a discussion of the larval characters of the Crangonidae (Crustacea, Decapoda, Caridea). *Bulletin of National Research Institute of Aquaculture*:1-12.
 13. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 14. KRYGIER, E. E., and H. F. HORTON. 1975. Distribution, reproduction, and growth of *Crangon nigracuda* and *Crangon franciscorum* in Yaquina Bay, Oregon. *Northwest Sciences*. 49:216-240.
 15. KURIS, A. M., and J. T. CARLTON. 1977. Description of a new species, *Crangon handi*, and new genus, *Lissocrangon*, of crangonid shrimps (Crustacea, Caridea) from California coast, with notes on adaptation in body shape and coloration. *Biological Bulletin*. 153:540-559.
 16. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 17. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 18. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. Invertebrate zoology: a functional evolutionary approach. Thomson Brooks/Cole, Belmont, CA.
 19. SCHMITT, W. L. 1921. The marine decapod crustacea of California. University of California Publications in Zoology. 23:1-470.
 20. SIEGFRIED, C. A. 1989. Species profiles, life histories, and environmental requirements of coastal fishes and invertebrates: Pacific southwest crangonid shrimp. U. S. Fish and Wildlife Service Biological Report. 82:1-18.
 21. SIMENSTAD, C. A., L. F. SMALL, and C. D. MCINTIRE. 1990. Consumption

- process and food web structure in the Columbia River estuary. *Progress in Oceanography*. 25:271-297.
22. SITTS, R. M., and A. W. KNIGHT. 1979. Predation by the estuarine shrimps *Crangon franciscorum* (Stimpson) and *Palaemon macrodactylus* (Rathbun). *Biological Bulletin*. 156:356-368.
 23. STRATHMANN, M. F. 1987. Phylum or Subphylum Crustacea Class Malacostraca Order Decapoda, Caridea, p. 432-440. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle.
 24. WAHLE, R. A. 1985. The feeding ecology of *Crangon franciscorum* and *Crangon nigricauda* in San Francisco Bay, California. *Journal of Crustacean Biology*. 5:311-326.
 25. WICKSTEN, M. K. 2011. Decapod Crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

Lissocrangon stylirostris

Common shrimp

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Caridea
Family: Crangonidae

Taxonomy: Schmitt (1921) described many shrimp in the genus *Crago* (e.g. *Crago alaskensis* and *C. franciscorum*) and reserved the genus *Crangon* for the snapping shrimp (now in the genus *Alpheus*). In 1955–56, the International Commission on Zoological Nomenclature formally reserved the genus *Crangon* for the sand shrimps only. Kuris and Carlton (1977) designated the new, and currently monotypic, genus *Lissocrangon* based on a lack of gastric carapace spines. Known synonyms for *L. stylirostris* include *Crago stylirostris* and *Crangon stylirostris* (Wicksten 2011).

Description

Size: Type specimen 55 mm in body length (Ricketts and Calvin 1971) with average length 30–61 mm (male average 43 mm and female 61 mm, Wicksten 2011; size range 20–70 mm for females, 15–49 mm for males, Marin Jarrin and Shanks 2008). This specimen (from Coos Bay) is 55 mm in length.

Color: White with black and brown chromatophores, giving gray appearance (see Fig. 23.11, Chace and Abbott 1980).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**). The body is laterally compressed and shrimp-like in the Caridea. The abdomen and associated appendages are outstretched and the abdomen usually has a sharp bend, which is less prominent in *L. stylirostris* (Kuris et al. 2007).

Cephalothorax:

Eyes: Small, pigmented and not covered by carapace.

Antennae: Antennal scale (scaphocerite) short, just a little over half the length of the carapace, blade with oblique inner margin; spine longer than blade (Fig. 2). Stylocerite (basal, lateral spine on antennule) longer than first antennular peduncle segment and blade-like (Wicksten 2011).

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004). Third maxilliped stout (particularly first segment, which is broadly dilated) and with exopod (Kuris and Carlton 1977; Wicksten 2011).

Carapace: Thin and smooth, without medial spine (*Lissocrangon*, Kuris and Carlton 1977). A pair of hepatic (lateral) spines with carinae or ridges (Fig 1). Also branchiostegal spines (Wicksten 2011).

Rostrum: Short, narrow with pointed tip that is sharply recurved and grooved (Wicksten 2011), length reaches end of eyes.

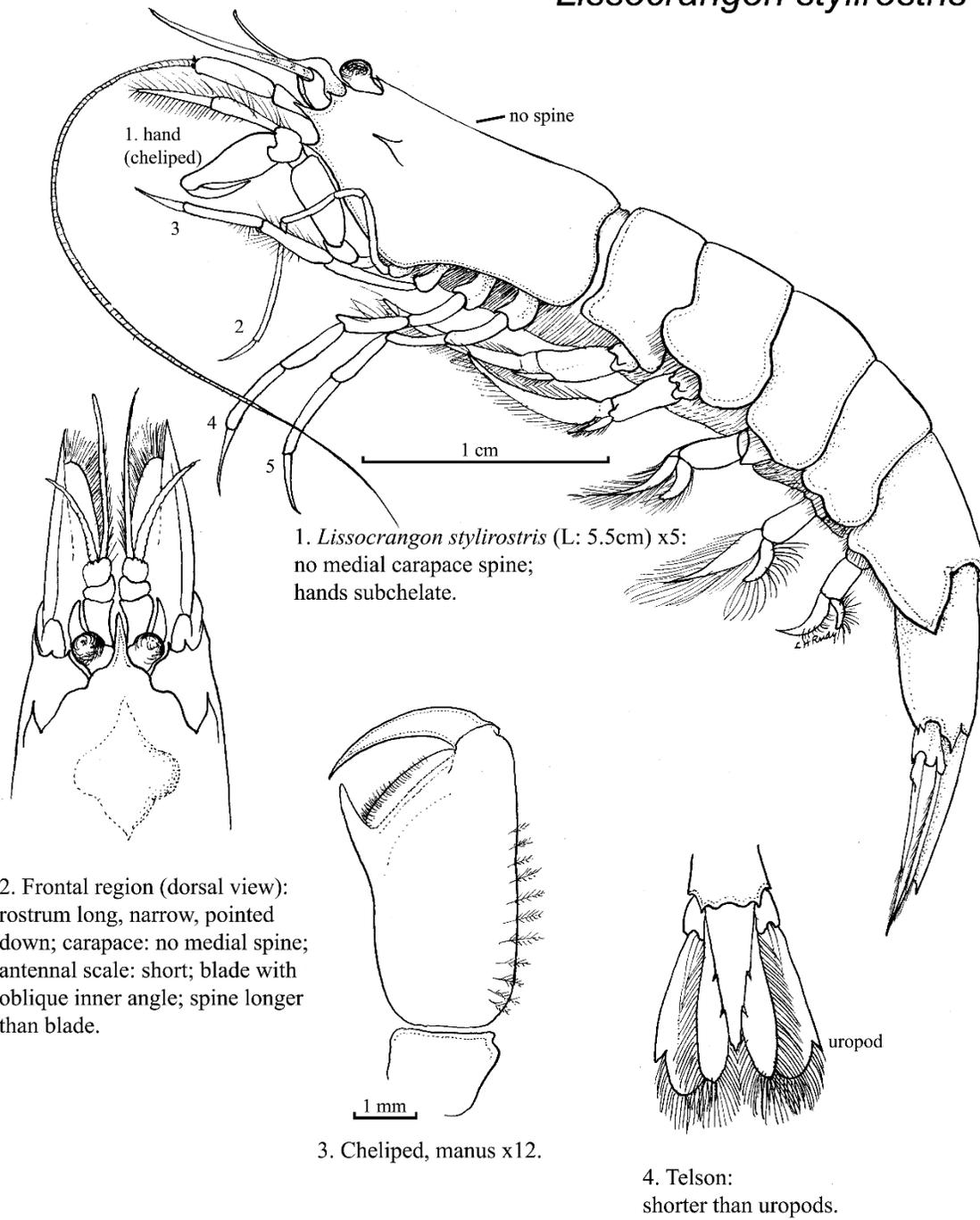
Teeth:

Pereopods: First pereopod stout and bearing spines on merus (one) and carpus (two), propodus widening distally and dactyl obliquely transverse when flexed. Second to fifth pereopod morphology as follows: second pereopod slender and chelate; third slender and with simple dactyl; fourth and fifth larger than third and with flattened dactyls (Wicksten 2011).

Chelipeds: Hands (manus) subchelate, slightly widened distally and about twice as long as wide (Fig. 3).

Abdomen (Pleon): Shrimp-like (Fig. 1). Male abdomen narrow (see **Sexual Dimorphism**). Morphology of the sixth abdominal segment is taxonomically significant and in *L. stylirostris* it bears a postero-ventral spine, no ventral groove and no carinae (Ricketts and Calvin 1971; Wicksten 2011).

Lissocrangon stylirostris



Telson & Uropods: Telson distinctly shorter than uropods and with four lateral spines (two pair) (Fig. 4) (Wicksten 2011).

Sexual Dimorphism: Females often have broader and larger bodies than males, which have compressed and squat bodies (Hoeman 1982; Marin Jarrin and Shanks 2008; Wicksten 2011). The size disparity between males and females could be the result of protandry (see **Reproduction**) (Marin Jarrin and Shanks 2008).

Possible Misidentifications

The family Crangonidae is characterized by first pereopods that are subchelate and second pereopods (if present) that are slender and equal in size, each with unsegmented carpus. Other characters include chela dactyls that close horizontally across the end of the propodus (“like the blade of a pocket knife” Wicksten 2011), a rostrum that is small and without spines and a body that is squat and somewhat depressed (although it can be broad in ovigerous females) (Wicksten 2011).

Three crangonid genera we revised in 1977 by Kuris and Carlton: *Lissocrangon*, *Crangon* and *Neocrangon*. Members of the two former genera are found locally. These genera can be differentiated by carapace spination: *Lissocrangon* lacks gastric spines, *Crangon* has one median gastric spine and *Neocrangon* (*Mesocrangon*, *M. munitella*, locally) has two gastric spines.

Crangon species have a straight and upturned rostrum and a telson that is of equal length or longer than uropods. The genus is divided into groups (i.e. subgenera, Kuris and Carlton 1977) based on characters of the sixth abdominal segment. In the first group, the sixth abdominal segment is smooth and lacks dorsal carinae (instead of two distal carinae). This group is further split based on a sulcate or convex sixth abdominal segment ventrum. The so-called “smooth, sulcate species group” (Kuris and Carlton 1977) includes all local *Crangon* species, *C. alaskensis*, *C. franciscorum*, *C. handi*, *C. nigricauda* and *C. nigromaculata*.

Besides lacking gastric spines, *Lissocrangon* species have a long narrow and sharply recurved rostrum, a telson that is shorter than the uropods and a sixth abdominal segment without a pair of dorsal carinae (keel-like ridges). This genus is

monotypic, the only known member is *L. stylirostris* (Kuris and Carlton 1977; Kuris et al. 2007).

Ecological Information

Range: Type locality is Trinidad, California. Known range includes Chirikof Island, Alaska to Todos Santos Bay, Baja California (Wicksten 2011).

Local Distribution: Coos Bay sites include Pt. Adams beach, at the mouth of South Slough.

Habitat: Often along high-energy sandy beaches, surf zone or semi-protected beaches (Kuris and Carlton 1977; Wicksten 2011). *Lissocrangon stylirostris* is a bottom-dweller that prefers hard sand (Ricketts and Calvin 1971) and occurs in the low tide, swash zone of Oregon beaches (see Figs. 1–3, McLauchlan 1990).

Salinity: Collected at 30 with range reported from salinities of 17 to 33 (Chace and Abbott 1980).

Temperature: 8.7–16°C (Chace and Abbott 1980).

Tidal Level: Intertidal to 80 m.

Associates: Can be infested with bopyrid isopod *Argeia pugettensis* (Butler 1980). This isopod is found next to the branchial chamber in many crangonids and forms a conspicuous bulge in the carapace (see Plate 19, Kozloff 1993; Wicksten 2011). In 2008, 61.7% of *L. stylirostris* were infected with the parasite and their reproductive output was negatively affected (Bastendorff Beach, Charleston, OR, Marin Jarrin and Shanks 2008). The crangonid shrimps *L. stylirostris* and *Crangon franciscorum* may also be infected with the microsporidium parasite *Pleistophora crangoni*, which occurs within their skeletal musculature (Breed and Olson 1977).

Abundance: Common in surf zone of semi-protected sandy beaches (Schmitt 1921). Densities ranged from 17–472 individuals per 100 m² at Bastendorff Beach, Charleston, OR, with highest density observed at night (Marin Jarrin and Shanks 2011).

Life-History Information

Reproduction: Many crangonid shrimp species are considered gonochoristic, but evidence suggests that some species exhibit protandry (Bauer 2004). Identifying ovigerous females is easy because female crangonid shrimp carry eggs which are attached with

between the joints and rami of the inner pleopods, under the abdomen (Siegfried 1989). Females ovigerous year-round (Grays Harbor, Washington, Hoeman 1982). Little is known about the reproduction and development in *L. stylirostris*.

Larva: In caridean shrimp species development proceeds through several zoea larval stages (Guerao and Cuesta 2014). Crangonid zoea are characterized by a wide rostrum, hemispherical eyestalks, antennule bases that touch, unsegmented antennule scales with inner flagellum having a setose spine, an exopod present on pereopod one (not 3–5), which is subchelate and a telson that widens posteriorly (see Fig. 48.1, Guerao and Cuesta 2014; Puls 2001).

Juvenile:

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: Feeds on small invertebrates and moves into the surf zone at night when its preferred prey, *Archaeomysis grebnitzkii* is most abundant (Marin Jarrin and Shanks 2011).

Predators: Commercially harvested in San Francisco Bay, California for bait with *C. franciscorum*, *C. nigricauda* and *C. nigromaculata*. Annual catches ranged from 320,000–1,360,000 kg (1940–1957) to 2,300–25,000 kg (1980s) per year (Chace and Abbott 1980).

Behavior:

Bibliography

1. BAUER, R. T. 2004. Remarkable shrimps: adaptations and natural history of the carideans. *Animal Natural History Series*. 7:1-282.
2. BREED, G. M., and R. E. OLSON. 1977. Biology of microsporidan parasite *Pleistophora crangonin* n.sp. in three species of crangonid sand shrimps. *Journal of Invertebrate Pathology*. 30:387-405.
3. CHACE, F. A., D. P. ABBOTT, R. H. MORRIS, and E. C. HADERLIE. 1980. Caridea: the shrimps. *In: Intertidal invertebrates of California*. Stanford University Press, Stanford, CA.
4. GUERAO, G., and J. A. CUESTA. 2014. Caridea, p. 250-255. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
5. HOEMAN, J. C. 1982. The distribution and ecology of three species of crangonid shrimp in Grays Harbor, Washington, and their susceptibility to entrainment by dredges. M.S. University of Washington.
6. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
7. KURIS, A. M., and J. T. CARLTON. 1977. Description of a new species, *Crangon handi*, and new genus, *Lissocrangon*, of crangonid shrimps (Crustacea, Caridea) from California coast, with notes on adaptation in body shape and coloration. *Biological Bulletin*. 153:540-559.
8. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
9. MARIN JARRIN, J. R., and A. L. SHANKS. 2008. Ecology of a population of *Lissocrangon stylirostris* (Caridea, Crangonidae), with notes on the occurrence and biology of its parasite, *Argeia pugettensis* (Isopoda, Bopyridae). *Journal of Crustacean Biology*. 28:613-621.
10. —. 2011. Spatio-temporal dynamics of the surf-zone faunal assemblages at a southern Oregon sandy beach. *Marine Ecology*. 32:232-242.
11. MCLACHLAN, A. 1990. Dissipative beaches and macrofauna communities on exposed intertidal sands. *Journal of Coastal Research*. 6:57-71.
12. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In:*

- Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
13. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 14. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*. Thomson Brooks/Cole, Belmont, CA.
 15. SCHMITT, W. L. 1921. The marine decapod crustacea of California. *University of California Publications in Zoology*. 23:1-470.
 16. SIEGFRIED, C. A. 1989. Species profiles, life histories, and environmental requirements of coastal fishes and invertebrates: Pacific southwest crangonid shrimp. U. S. Fish and Wildlife Service Biological Report. 82:1-18.
 17. WICKSTEN, M. K. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

Heptacarpus paludicola

A broken back shrimp

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Caridea
Family: Thoridae

Taxonomy: Local *Heptacarpus* species (e.g. *H. paludicola* and *H. sitchensis*) were briefly considered to be in the genus *Spirontocaris* (Rathbun 1904; Schmitt 1921). However members of *Spirontocaris* have two or more supraorbital spines (rather than only one in *Heptacarpus*). Thus a known synonym for *H. paludicola* is *S. paludicola* (Wicksten 2011).

Description

Size: Individuals 20 mm (males) to 32 mm (females) in length (Wicksten 2011).

Illustrated specimen was a 30 mm-long, ovigerous female collected from the South Slough of Coos Bay.

Color: Variable across individuals. Uniform with extremities clear and green stripes or speckles. Color can be deep blue at night (Bauer 1981). Adult color patterns arise from chromatophores under the exoskeleton and are related to animal age and sex (e.g. mature and breeding females have prominent color patterns) (Bauer 1981). Five morphs were described by Bauer (1981) for both *H. sitchensis* and *H. paludicola*, including four color morphs and one transparent morph. Adults may exhibit camouflaging colors based on surrounding algae (Bauer 1981), but color patterns may be more or less fixed (genetically) and variably expressed in different environments (Bauer 1982).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**) (Kuris et al. 2007). The abdomen and associated appendages are outstretched in *Heptacarpus* species and the abdomen usually has a sharp bend (“broken-back shrimp” Kozloff 1993).

Cephalothorax:

Eyes:

Antennae: Antennal scale never much longer than rostrum. Antennular peduncle bears spines on each of the three

segments and stylocerite (basal, lateral spine on antennule) does not extend beyond the first segment (Wicksten 2011).

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004). Third maxilliped without exopodite and with epipods (Fig. 1). Mandible with incisor process (Schmitt 1921).

Carapace: No supraorbital spines (*Heptacarpus*, Kuris et al. 2007; Wicksten 2011) and no lateral or dorsal spines.

Rostrum: Well-developed, longer than carapace, extending beyond antennular peduncle (Fig. 2). Rostral teeth include both dorsal (6–8, seven in current specimen, Fig. 1) and ventral (2–4, two in current specimen, Fig. 1). Dorsal edge of rostrum straight, not curved with anterior teeth.

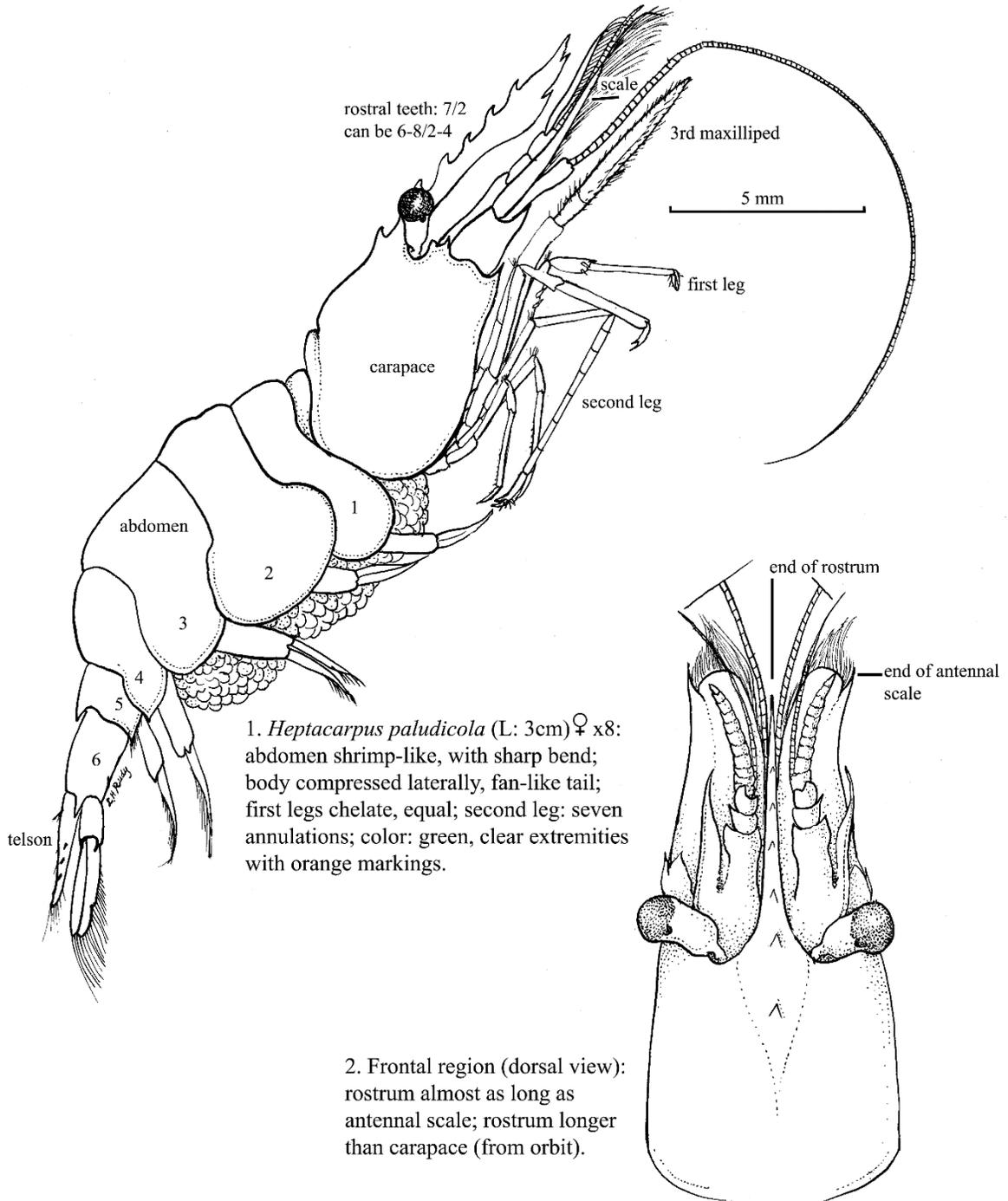
Teeth: Rostral teeth present (see **Rostrum**).

Pereopods: Pereopods 1–2 with epipods. Epipod morphology is particularly relevant to the genus *Heptacarpus* and species with a higher number are considered ancestral to the group (Bauer 1984b). Pereopods 3–5 with bifid dactyls with spines arranged as follows: merus of pereopod three with five spines, pereopod four with four spines and pereopod five with 2–4 spines (Wicksten 2011). Second legs chelate, nearly equal, with seven annulations on carpus (Fig. 1).

Chelipeds: Equal, chelate (Fig. 1).

Abdomen (Pleon): Shrimp-like, with fantail, body laterally compressed. Side plates of second segment overlap those of first with sharp bend (Fig. 1). The third segment without hump and the sixth segment is shorter than telson (Fig. 1). Segments 1–3 with pleura that is rounded, fourth segment with tooth and fifth with spine (Wicksten 2011).

Heptacarpus paludicola



Telson & Uropods: Telson bears 4–5 pairs of dorso-lateral spines (Wicksten 2011) (Fig. 1).

Sexual Dimorphism: Females often have broader and larger bodies than males, which have compressed and squat bodies (Wicksten 2011).

Possible Misidentifications

The family Hippolytidae was split into three families following a cladistic analysis by Christoffersen (1987) that are currently recognized by some (e.g. Wicksten 2011), but not all authors (e.g. Kuris et al. 2007). These three families include the Lysmatidae, Hippolytidae and Thoridae. The Lysmatidae are characterized by very long antennular flagella. The three families can further be distinguished by the number of carpal articles on the second pereopod: 22 or more in Lysmatidae, three in Hippolytidae and seven in Thoridae. In addition, Thoridae and Hippolytidae can be differentiated by their supraorbital spines, one in the latter and 0–4 in the former family (Wicksten 2011). The Lysmatidae is represented by a single species locally, *Lysmata californica* (Kuris et al. 2007; Wicksten 2011). When following the above taxonomy (Christoffersen 1987; Wicksten 2011), local members of the Hippolytidae include *Hippolyte californiensis* and *H. clarki*. Meanwhile, the genus *Heptacarpus*, with eleven local species, falls within the Thoridae, as do the local species *Lebbeus lagunae* and *Spirontocaris prionota* (Kuris et al. 2007; Wicksten 2011).

Very close in color, morphology, and habitat preference is *Heptacarpus sitchensis*, whose adult rostral teeth are 4–8/0–5, but whose rostrum, while it can reach to the middle of the antennal scale, does not reach to the end of the scale as does that of *H. paludicola*. The rostral teeth are closer together on *H. sitchensis* and the rostrum is more slender (Schmitt 1921), as well as being only equal to or shorter than the carapace. Our *H. sitchensis* specimens were only 1.5 cm, half the size of the female *H. paludicola*. *Heptacarpus sitchensis* is the most commonly found transparent shrimp in tide pools (Ricketts and Calvin 1971), while *H. paludicola* is more common in mudflats and in eelgrass.

Heptacarpus taylori, also has a short rostrum, reaching just to the eye and is often

brightly colored, with a series of teeth from anterior carapace margin to the apex.

Heptacarpus brevirostris, with smooth rostrum (without lower teeth) that reaches only the first segment of the antennal peduncle. The merus of *H. brevirostris* has a single spine on pereopods 3–4. *Heptacarpus palpator* is similar to *Heptacarpus brevirostris*, but with a longer rostrum that can be di- or trifid, and a longer antennal scale (Wicksten 1986).

Heptacarpus stimpsoni, from Puget Sound, has rostrum that extends over eye (only slightly), with dorsal teeth and pereopod (3–5) dactyls that are simple and curved.

Heptacarpus carinatus is a long-rostrumed shrimp, with distal rostral teeth (3–7 dorsal and 2–6 ventral) and epipods present on pereopods 1–3. *Heptacarpus franciscanus*, from San Francisco Bay, has a rostrum longer than the carapace. *Heptacarpus pugettensis*, *H. flexus*, and *H. tenuissimus* have a hump on the third abdominal segment. *Heptacarpus pugettensis* has epipods on pereopods 1–2 and a rostrum that just reaches the end of the first segment of antennular peduncle and not beyond. *Heptacarpus flexus* is morphologically similar to *H. carinatus*, but with epipods on pereopods 1–2 only and a narrow rostrum with teeth (4–5 dorsal and 5–8 ventral). *Heptacarpus tenuissimus* lacks teeth on the ventrum of the fourth abdominal pleon and also lacks an exopod on the third maxilliped (see dichotomous key in Wicksten 2011 for *Heptacarpus* species).

Ecological Information

Range: Type locality is Humboldt Bay, California. Known range includes Tava Island, Alaska to San Diego, California (Schmitt 1921; Wicksten 2011).

Local Distribution: Coos Bay distribution near, and south of, the Charleston Bridge in South Slough.

Habitat: South Slough amongst mud and eelgrass (*Zostera*, *Ulva*), also on pilings, floats and in tide pools of outer coasts (Kuris et al. 2007; Wicksten 2011).

Salinity: Collected at salinity 30.

Temperature:

Tidal Level: Collected at +0.15 m and is intertidal to 10 m depths (Wicksten 2011).

Associates:

Abundance: Common to abundant (Schmitt 1921; Kuris et al. 2007).

Life-History Information

Reproduction: Ovigerous female found in March, in South Slough, Coos Bay. Males and females may be (weakly) attracted to each other with sex pheromones (Bauer 1979), but are generally only triggered to initiate copulation after physical contact (Bauer 2011). Little is known about the development in *Heptacarpus* species (Strathmann 1987; Puls 2001).

Larva: Larval development in *Heptacarpus* species proceeds via a series of zoea, and, a final, post-zoea (decapodid) stage, each marked by a molt (Puls 2001; Guerao and Cuesta 2014). The zoea are planktotrophic, have a narrow rostrum (without teeth), cylindrical eyestalks, antennule bases that are close together (but not touching), and abdomen with postero-lateral spines (Puls 2001; see Fig. 48.3, Guerao and Cuesta 2014).

Juvenile:

Longevity:

Growth Rate:

Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: Carnivorous (Kozloff 1993). The majority of caridean shrimps are omnivorous (Chace and Abbott 1980).

Predators: Fish.

Behavior: Propel themselves backward by flexing their tails forward and often flip out of a collector's hand. Members of the genus *Heptacarpus* have been shown to exhibit body, gill and embryo grooming in response to microbial fouling and parasites. Grooming with specialized antennal brushes is found in members of the Stenopodidea, Caridea and Dendrobranchiata and suggests a common ancestor rather than evolutionary convergence (see Bauer 1989).

Bibliography

1. BAUER, R. T. 1979. Sex attraction and recognition in the caridean shrimp *Heptacarpus Paludicola* (Holmes)
2. —. 1981. Color patterns of the shrimps *Heptacarpus pictus* and *Heptacarpus paludicola* (Caridea, Hippolytidae). *Marine Biology*. 64:141-152.
3. —. 1982. Polymorphism of color pattern in the caridean shrimps *Heptacarpus pictus* and *Heptacarpus paludicola*. *Marine Behaviour and Physiology*. 8:249-265.
4. —. 1984. Morphological trends in the genus *Heptacarpus* (Decapoda, Caridea) and their phylogenetic significance. *Journal of Crustacean Biology*. 4:201-225.
5. —. 1989. Decapod crustacean grooming: functional morphology, adaptive value, and phylogenetic significance. *Crustacean Issues*. 6:49-73.
6. —. 2011. Chemical communication in decapod shrimps the influence of mating and social systems on the relative importance of olfactory and contact pheromones. *Chemical Communication in Crustaceans*:277-296.
7. CHACE, F. A., D. P. ABBOTT, R. H. MORRIS, and E. C. HADERLIE. 1980. Caridea: the shrimps. *In: Intertidal invertebrates of California*. Stanford University Press, Stanford, CA.
8. CHRISTOFFERSEN, M. L. 1987. Phylogenetic relationships of hippolytid genera with an assignment of new families for the Crangonoidea and Alpheoidea (Crustacea, Decapoda, Caridea). *Cladistics*. 3:348-362.
9. GUERAO, G., and J. A. CUESTA. 2014. Caridea, p. 250-255. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
10. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
11. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal*

- invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
12. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 13. RATHBUN, M. J. 1904. Decapod crustaceans of the northwest coast of North America. Harriman Alaska Expedition. x:1-210.
 14. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 15. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*. Thomson Brooks/Cole, Belmont, CA.
 16. SCHMITT, W. L. 1921. The marine decapod crustacea of California. *University of California Publications in Zoology*. 23:1-470.
 17. STRATHMANN, M. F. 1987. Phylum or Subphylum Crustacea Class Malacostraca Order Decapoda, Caridea, p. 432-440. *In*: *Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle.
 18. WICKSTEN, M. K. 1986. A new species of *Heptacarpus* from California, USA with a re-description of *Heptacarpus palpator* (Owen) (Caridea: Hippolytidae). *Bulletin Southern California Academy of Sciences*. 85:46-55.
 19. —. 2011. Decapod Crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.

Updated 2015

Heptacarpus sitchensis

A broken back shrimp, glass shrimp

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Decapoda
Section: Caridea
Family: Thoridae

Taxonomy: A re-examination of 263 preserved specimens revealed that *H. pictus*, previously considered a different species, is a junior synonym of *H. sitchensis* based the presence of epipods on the first and second pereopods and third maxillipeds (Wicksten et al. 1996; Wicksten 2011). Local *Heptacarpus* species were also briefly considered to be in the genus *Spirontocaris*, however members of the latter genus have two or more supraorbital spines (rather than only one in *Heptacarpus*) (Wicksten 2011). Additional synonyms for *Heptacarpus sitchensis* include *S. picta*, *S. sitchensis*, and *H. picta*.

Description

Size: Individuals 16 mm (males) to 28 mm (females) in length (Wicksten 2011). This specimen (from South Slough of Coos Bay) is 15 mm long.

Color: Transparent, with orange or brown lines (longitudinal stripes), green at leg bases and black eyes (Chace and Abbott 1980; Wicksten 2011). Adult color patterns arise from chromatophores under the exoskeleton and are related to the age and sex of the individual (e.g. mature and breeding females have prominent color patterns) (Bauer 1981). Five morphs were described by Bauer (1981) for both *H. sitchensis* and *H. paludicola*, including four color morphs and one transparent morph. The most extreme variation in color was seen in *H. sitchensis*. Adults may exhibit camouflaging colors based on surrounding algae (Bauer 1981), but color patterns may be more or less fixed (genetically) and variably expressed in different environments (Bauer 1984a).

General Morphology: The body of decapod crustaceans can be divided into the **cephalothorax** (fused head and thorax) and **abdomen**. They have a large plate-like carapace dorsally, beneath which are five pairs of thoracic appendages (see **chelipeds** and **pereopods**) and three pairs of maxillipeds (see **mouthparts**) (Kuris et al. 2007). The abdomen and associated appendages are outstretched in *Heptacarpus*

species and the abdomen usually has a sharp bend (“broken-back shrimp” Kozloff 1993).

Cephalothorax:

Eyes:

Antennae: First segment of the antennular peduncle bears spine and stylocerite (basal, lateral spine on antennule) meets or exceeds the length of the first segment (Wicksten 2011) (Fig. 4).

Mouthparts: The mouth of decapod crustaceans comprises six pairs of appendages including one pair of mandibles (on either side of the mouth), two pairs of maxillae and three pairs of maxillipeds. The maxillae and maxillipeds attach posterior to the mouth and extend to cover the mandibles (Ruppert et al. 2004). Third maxilliped without exopodite and with epipods (Schmitt 1921; Wicksten 2011).

Carapace: No supraorbital or other spines (*Heptacarpus*).

Rostrum: Well developed and shorter than carapace, barely exceeding the length of the antennular peduncle (Fig. 4). Rostral teeth are slender and close together (Schmitt 1921) and include both dorsal (4–8, seven in present specimen, Fig. 1) and ventral (0–5, three in present specimen, Fig. 1) teeth (Fig. 1) (Wicksten 2011).

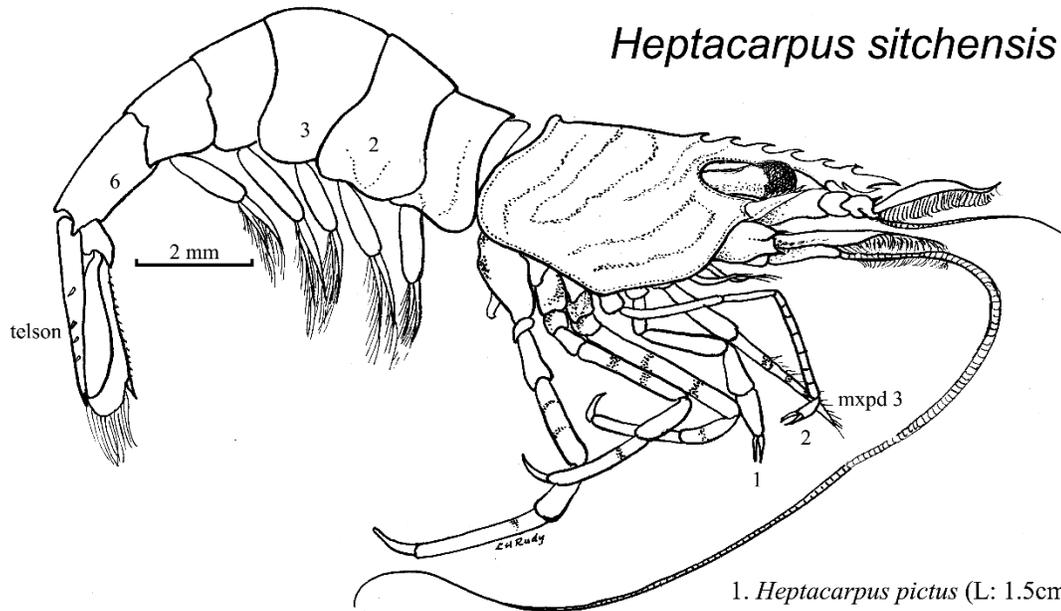
Teeth: Rostral teeth present (see **Rostrum**).

Pereopods: Epipods present on pereopods 1–2. Epipod morphology is particularly relevant to the genus *Heptacarpus* and species with a higher number are considered ancestral to the group (Bauer 1984b). Pereopods 3–5 have bifid dactyls and are thick and bear spines (merus of pereopod three with 0–9 spines; pereopods four and five with 0–5 spines) (Fig. 3) (Wicksten 2011).

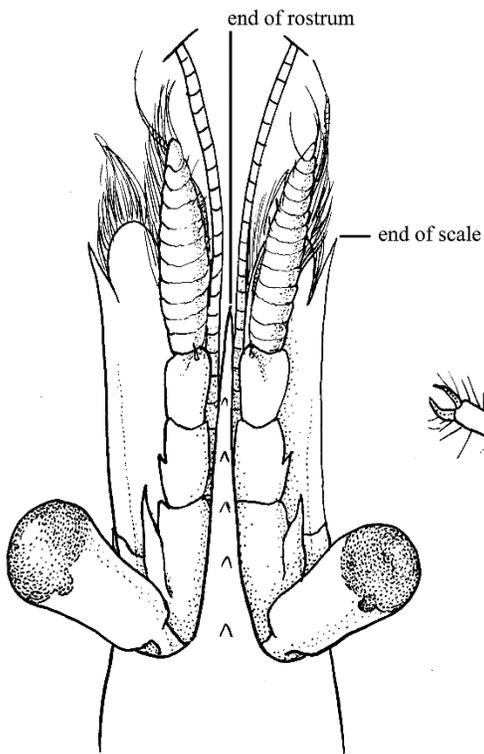
Chelipeds: Equal and chelate (Fig. 2).

Abdomen (Pleon): Shrimp-like, with fan tail, and laterally compressed body. The side plates of the second segment overlap those of the first with sharp bend. The third segment is without hump and the sixth

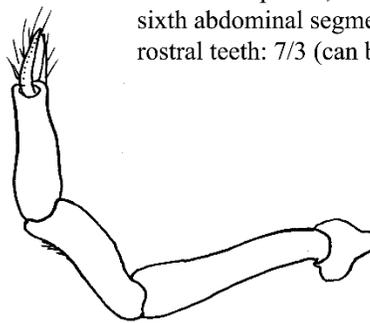
Heptacarpus sitchensis



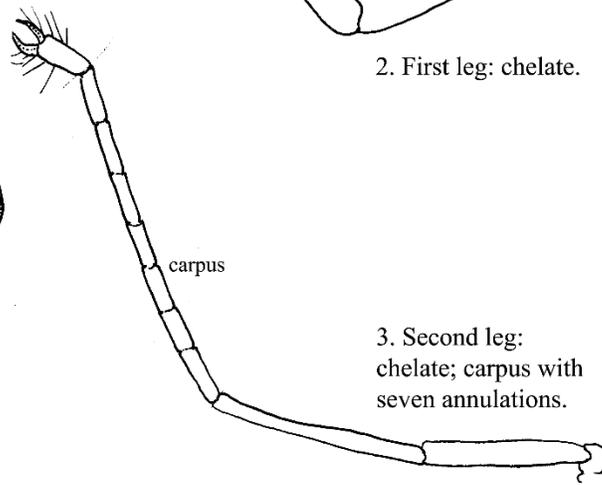
1. *Heptacarpus pictus* (L: 1.5cm) x10:
 color: transparent, green leg bases, red
 striped legs, carapace; third maxilliped
 without exopodite; telson longer than
 sixth abdominal segment;
 rostral teeth: 7/3 (can be 4-8/0-5).



4. Frontal region (dorsal view):
 rostrum narrow at eyes; rostrum
 more than half length of scale,
 but not to the end; rostrum (from
 posterior of orbit) shorter than
 carapace.



2. First leg: chelate.



3. Second leg:
 chelate; carpus with
 seven annulations.

segment shorter is than telson (Fig. 1). Pleura of segments 1–3 are rounded and segments 4–5 bear a postero-lateral tooth (Wicksten 2011).

Telson & Uropods: Telson bears 4–5 pairs of dorso-lateral spines (Wicksten 2011).

Sexual Dimorphism: Females often have broader and larger bodies than males, which have compressed and squat bodies (Wicksten 2011). It is unknown if carapace spines are consistently sexually dimorphic, but male *H. sitchensis* appear to differ from females in that they lack a pterygostomial spine. In fact, this character once defined the two species *H. littoralis* (lacking pterygostomial spine) and *H. sitchensis* (bearing pterygostomial spine), until recent evidence revealed that *H. littoralis* was simply male *H. sitchensis* individuals (Stamatious and Jensen 2004).

Possible Misidentifications

The family Hippolytidae was split into three families in a cladistic analysis by Christoffersen (1987) that are currently recognized by some (Wicksten 2011), but not all authors (e.g. Kuris et al. 2007). These three families include the Lysmatidae, Hippolytidae and Thoridae. The Lysmatidae are characterized by very long antennular flagella. The three families can further be divided by the number of carpal articles on the second pereopod: 22 or more in Lysmatidae, three in Hippolytidae and seven in Thoridae. In addition, Thoridae and Hippolytidae can be differentiated by their supraorbital spines, one in the latter and 0–4 in the former family (Wicksten 2011). The Lysmatidae is represented by a single species locally, *Lysmata californica* (Kuris et al. 2007; Wicksten 2011). When following the above taxonomy (Christoffersen 1987; Wicksten 2011), local members of the Hippolytidae include *Hippolyte californiensis* and *H. clarki*. Meanwhile, the genus *Heptacarpus*, with eleven local species, falls within the Thoridae as do the local species *Lebbeus lagunae* and *Spirontocaris prionota* (Kuris et al. 2007; Wicksten 2011).

Heptacarpus sitchensis is morphologically most similar to the green *Zostera* dweller *H. paludicola*, with a difference chiefly in the length of the rostrum. In *H. sitchensis*, the rostrum does not reach the end of the antennular peduncle, but in *H.*

paludicola the rostrum reaches and often extends beyond the antennular peduncle (Wicksten 2011). Our *H. sitchensis* specimens were only 1.5 cm, half the size of the female *H. paludicola*. *Heptacarpus sitchensis* is the most commonly found transparent shrimp in tide pools (Ricketts and Calvin 1971), while *H. paludicola* is more common in mudflats and in eelgrass.

Heptacarpus taylori, also has a short rostrum, reaching just to the eye and is often brightly colored and with a series of teeth from anterior carapace margin to the apex. *Heptacarpus brevirostris*, with smooth rostrum (without lower teeth) that reaches only the first segment of the antennal peduncle. The merus of *H. brevirostris* has a single spine on pereopods 3–4. *Heptacarpus palpator*, is similar to *Heptacarpus brevirostris*, but with a longer rostrum that can be di- or trifid, and a longer antennal scale (Wicksten 1986). *Heptacarpus stimpsoni*, from Puget Sound, whose rostrum extends over eye (only slightly), with dorsal teeth and pereopod (3–5) dactyls that are simple and curved. *Heptacarpus carinatus* is a long-rostrumed shrimp, with distal rostral teeth (3–7 dorsal and 2–6 ventral) and epipods present on 1–3 pereopods. *Heptacarpus franciscanus*, from San Francisco Bay, has a rostrum longer than the the carapace. *Heptacarpus pugettensis*, *Heptacarpus flexus*, and *H. tenuissimus* have a hump on the third abdominal segment. *Heptacarpus pugettensis* has epipods on pereopods 1–2 and a rostrum that only just reaches the end of the first segment of antennular peduncle. *Heptacarpus flexus* is morphologically similar to *H. carinatus*, but with epipods on pereopods 1–2 only and a narrow rostrum with teeth (4–5 dorsal and 5–8 ventral). *Heptacarpus tenuissimus* lacks teeth on the ventrum of the fourth abdominal pleon as well as an epipod on the third maxilliped (see dichotomous key in Wicksten 2011 for *Heptacarpus* species).

Ecological Information

Range: Type locality is Sitka, Alaska. Known range includes resurrection Bay, Alaska to Baja California, Mexico (Wicksten 2011).

Local Distribution: Coos Bay distribution near the Charleston Bridge in South Slough.

Habitat: Most commonly occurring, transparent shrimp in rock pools (Ricketts and Calvin 1971) and also in *Zostera* beds (South

Slough mudflats) and on floats (Kuris et al. 2007).

Salinity: Collected at salinity 30.

Temperature:

Tidal Level: Collected from +0.15 m to 12 m depths, although rarely (Wicksten 2011).

Associates: Individuals often associated with a variety of polychaete species.

Abundance: Abundant to common (Kuris et al. 2007).

Life-History Information

Reproduction: Females ovigerous in May, June and September (Butler 1980; Puget Sound, Washington, Stamatiou and Jensen 2004). Males and females may be (weakly) attracted to each other with sex pheromones (Bauer 1979), but copulation is generally only initiated after physical contact (Bauer 2011). Spermatophore deposition (from male pereopods 1–2) is beneath the first abdominal segment (Zhang and Lin 2004). Females produce multiple broods in one year, molting between broods (Chace and Abbott 1980). Little is known about the development in *Heptacarpus* species (Strathmann 1987; Puls 2001).

Larva: Larval development in *Heptacarpus* species proceeds via a series of zoea, and, a final, post-zoea (decapodid) stage, each marked by a molt (Puls 2001; Guerao and Cuesta 2014). The zoea are planktotrophic, have a narrow rostrum (without teeth), cylindrical eyestalks, antennule bases that are close together, and abdomen with postero-lateral spines (Puls 2001; see Fig. 48.3, Guerao and Cuesta 2014).

Juvenile:

Longevity:

Growth Rate: Growth occurs in conjunction with molting. In pre-molting periods the epidermis separates from the old cuticle and a dramatic increase in epidermal cell growth occurs. Post-molt individuals will have soft shells until a thin membranous layer is deposited and the cuticle gradually hardens. During a molt decapods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: The majority of caridean shrimps are omnivorous (Chace and Abbott 1980) and *H. sitchensis* individuals have an olfactory response to food, sensing food in nearby water (Bauer 2011).

Predators: Fish and sea spiders, in particular *Achelia simplissima* individuals as well as their egg masses (Burriss 2011).

Behavior: Members of the genus *Heptacarpus* have been shown to exhibit body, gill and embryo grooming in response to microbial fouling and parasites. Grooming with specialized antennal brushes is found in members of the Stenopodidea, Caridea and Dendrobranchiata and suggests a common ancestor rather than evolutionary convergence (see Bauer 1989).

Bibliography

1. BAUER, R. T. 1979. Sex attraction and recognition in the caridean shrimp *Heptacarpus Paludicola* (Holmes) (Decapoda, Hippolytidae). *Marine Behaviour and Physiology*. 6:157-174.
2. —. 1981. Color patterns of the shrimps *Heptacarpus pictus* and *Heptacarpus paludicola* (Caridea, Hippolytidae). *Marine Biology*. 64:141-152.
3. —. 1982. Polymorphism of color pattern in the caridean shrimps *Heptacarpus pictus* and *Heptacarpus paludicola*. *Marine Behaviour and Physiology*. 8:249-265.
4. —. 1984. Morphological trends in the genus *Heptacarpus* (Decapoda, Caridea) and their phylogenetic significance. *Journal of Crustacean Biology*. 4:201-225.
5. —. 1989. Decapod crustacean grooming: functional morphology, adaptive value, and phylogenetic significance. *Crustacean Issues*. 6:49-73.
6. —. 2011. Chemical communication in decapod shrimps: the influence of mating and social systems on the relative importance of olfactory and contact pheromones. *Chemical Communication in Crustaceans*:277-296.
7. BURRIS, Z. P. 2011. Costs of exclusive male parental care in the sea spider *Achelia simplissima* (Arthropoda: Pycnogonida). *Marine Biology*. 158:381-390.
8. BUTLER, T. H. 1980. Shrimps of the Pacific coast of Canada. *Canadian Bulletin of Fisheries and Aquatic Sciences*:1-280.

9. CHACE, F. A., D. P. ABBOTT, R. H. MORRIS, and E. C. HADERLIE. 1980. Caridea: the shrimps. *In: Intertidal invertebrates of California*. Stanford University Press, Stanford, CA.
10. CHRISTOFFERSEN, M. L. 1987. Phylogenetic relationships of hippolytid genera with an assignment of new families for the Crangonoidea and Alpheoidea (Crustacea, Decapoda, Caridea). *Cladistics*. 3:348-362.
11. GUERAO, G., and J. A. CUESTA. 2014. Caridea, p. 250-255. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
12. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
13. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
14. PULS, A. L. 2001. Arthropoda: Decapoda, p. 179-250. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
15. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
16. RUPPERT, E. E., R. S. FOX, and R. D. BARNES. 2004. *Invertebrate zoology: a functional evolutionary approach*. Thomson Brooks/Cole, Belmont, CA.
17. SCHMITT, W. L. 1921. *The marine decapod crustacea of California*. University of California Publications in Zoology. 23:1-470.
18. STAMATIOU, L., and G. C. JENSEN. 2004. *Heptacarpus littoralis* (Butler) a synonym of *Heptacarpus sitchensis* (Brandt) (Crustacea, Decapoda, Hippolytidae). *Zootaxa*:1-4.
19. STRATHMANN, M. F. 1987. Phylum or Subphylum Crustacea Class Malacostraca Order Decapoda, Caridea, p. 432-440. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle.
20. WICKSTEN, M. K. 1986. A new species of *Heptacarpus* from California, USA with a re-description of *Heptacarpus palpator* (Owen) (Caridea: Hippolytidae). *Bulletin Southern California Academy of Sciences*. 85:46-55.
21. —. 2011. Decapod crustacea of the Californian and Oregonian Zoogeographic Provinces. <http://escholarship.org/uc/item/7sk9t2dz>. Scripps Institution of Oceanography, UC San Diego, San Diego, CA.
22. WICKSTEN, M. K., R. FLYNN, and M. FAGARASON. 1996. *Heptacarpus pictus* (Stimpson) synonymized with *Heptacarpus sitchensis* (Brandt) (Decapoda, Hippolytidae). *Crustaceana*. 69:71-75.
23. ZHANG, D., and J. D. LIN. 2004. Mating without anterior pleopods in a simultaneous hermaphroditic shrimp, *Lysmata wurdemanni* (Decapoda, Caridea). *Crustaceana*. 77:1203-1212.

Updated 2015

Lamprops quadriplicata

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Cumacea
Family: Lampropidae

Description

Size: The holotype, described from Vancouver Island, was 11 mm in length (Hart 1930). The illustrated female (from Coos Bay) was 6 mm long (Fig. 1).

Color: Light brown, with dark brown on carapace and chromatophores (Hart 1930). However, Procter (1933) describes that the carapace can be divided by a diagonal line that is just posterior to the antero-ventral notch, with the anterior a greenish color and the posterior a deep brown (in Zimmer 1980). Descriptions of color in the Cumacea are difficult as many species were described based on preserved material, where the color fades.

General Morphology: Cumaceans are easily recognizable by a large and inflated carapace and a (relatively) slender, flexible thorax and abdomen (Kozloff 1993; Gerken and Martin 2014). Their bodies can be divided into these three major regions: the **cephalon** (head) that is covered by a **carapace** and includes the first five pairs of appendages (antennae, mandibles, maxillae, collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax), usually consisting of five thoracic somites, followed by the **pleon** (abdomen) with consistently six pleonites. The fifth pleonite is usually the longest and the pleonites are lacking **pleopods** in female individuals. The cumacean family Lampropidae is characterized by a freely articulating telson with three or more terminal setae (Watling 2007).

Cephalon: A carapace covers the cephalon and first three thoracic somites and is expanded on either side to form a branchial chamber (Watling 2007).

Carapace: Carapace is with four oblique parallel lines on each side (hence the name, *quadriplicata*) (Smith 1879) (Fig. 1). (Note: Fig. 3 is a close-up of *L. fasciata*, with only three parallel lines, for comparison.)

Rostrum: Two pseudorostral lobes (together called a pseudorostrum), or

extensions of the carapace, extend anteriorly but do not fuse in front of the head in cumaceans (Watling 2007). The pseudorostrum in female *L. quadriplicata* is short and obtuse (Sars 1900) (Fig. 1), while in males, it does not extend beyond anterolateral corners (Hart 1930) (Fig. 3).

Eyes: Female lacks eyes, as in most cumaceans (Fig. 1). Males, on the other hand, have well developed eyes (*Lamprops*, Sars 1900) (e.g. Fig. 3).

Antennae: The first antenna is well developed in females with 4–5 articles (Lampropidae, Fage 1951) (Fig. 1). The second antenna is short in females (not visible in Fig. 1). In males, the second antenna is with articulated flagellum that is rather prehensile, but is generally concealed and used for clasping in copulation (Sars 1900).

Mouthparts: Siphon of maxilliped clearly visible (Figs. 1) (other mouthparts not figured.)

Pereon: Consists of five thoracic somites, each with paired appendages (**pereopods**).

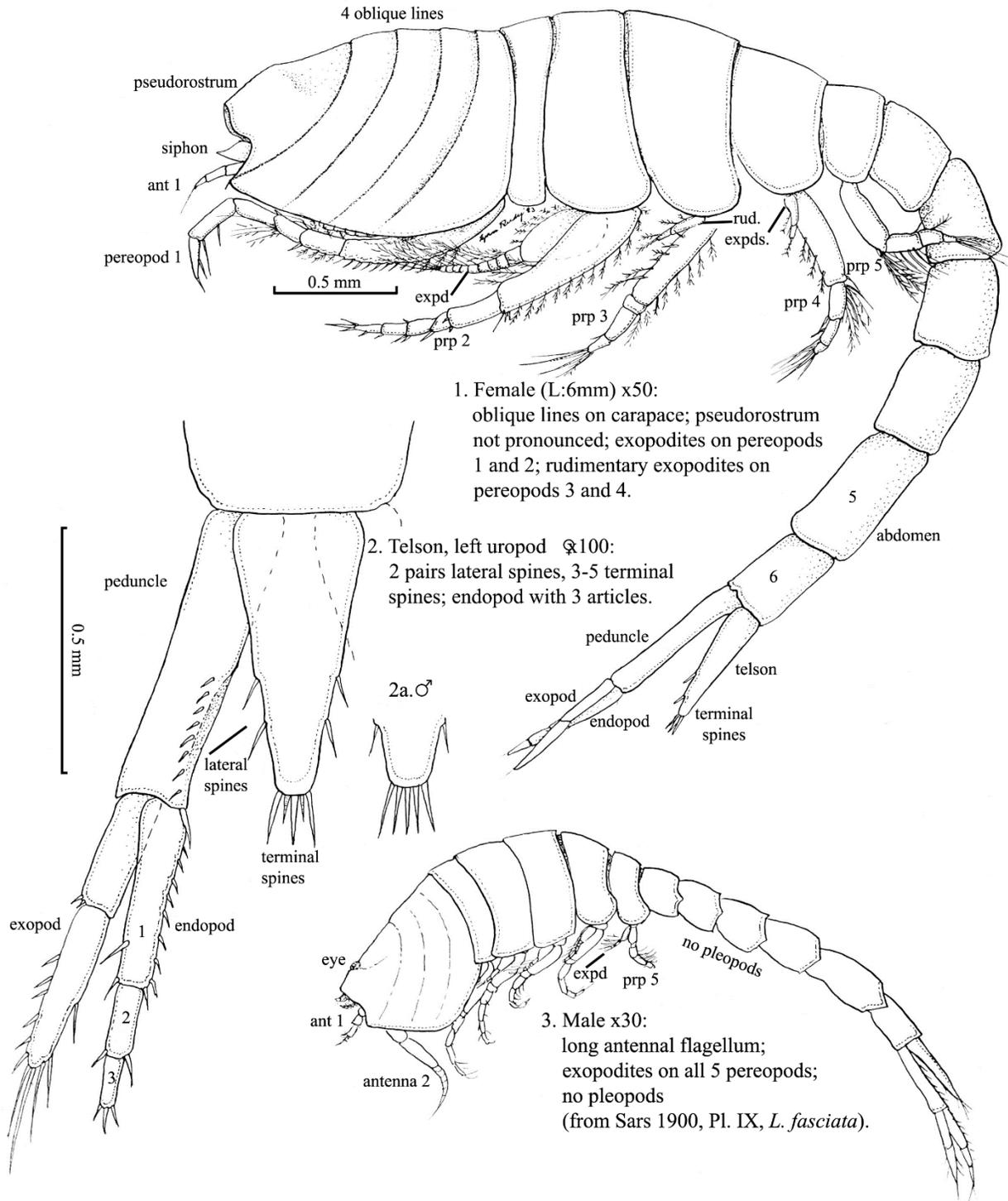
Pereopods: Female with exopodites on pereopods one and two and rudimentary exopodites on pereopods three and four (Fig. 1). Male exopodites on all five pereopods (Lampropidae, Watling 1979) (Fig. 3).

Pleon: Consists of six segments (Fig. 1).

Pleopods: All female cumaceans lack pleopods (Fig. 1) and males in the genus *Lamprops* are also lacking pleopods (Kozloff 1974) (Fig. 3).

Telson: Telson is free and distinct (compare to Leuconidae and Nannastacidae). Male telson has five terminal spines of about equal length (Watling 1979) (Fig. 2a) and females have 3–5 terminal spines, but they are not all equal in length (Kozloff 1974). The telson also has two to three pairs of lateral spines (two pairs in most females, Given 1965). The telson length is equal to or slightly longer than uropod peduncle (Smith 1879) and is truncate (Fig. 2).

Lamprops quadriplicata



1. Female (L:6mm) x50:
oblique lines on carapace; pseudorostrum not pronounced; exopodites on pereopods 1 and 2; rudimentary exopodites on pereopods 3 and 4.

2. Telson, left uropod ♀100:
2 pairs lateral spines, 3-5 terminal spines; endopod with 3 articles.

3. Male x30:
long antennal flagellum;
exopodites on all 5 pereopods;
no pleopods
(from Sars 1900, Pl. IX, *L. fasciata*).

Uropods: Uropod peduncles about equal to telson in length (Watling 2007; Smith 1879) and uropod endopods have three articles each (Lampropidae, Watling 1979) (Fig. 2). Cumacean uropod exopods are always biarticulate (Watling 1979).

Sexual Dimorphism: Females lack eyes and mature individuals can be recognized by the presence of a brood pouch. Female and immature individuals of both sexes have 3–5 apical telson spines, while males have five subequal spines. Five exopodites occur on pereopods in males compared to two exopodites, in addition to two rudimentary ones, in females. Males also have long second antennal flagella.

Possible Misidentifications

Cumaceans are very small (range 1 mm–1 cm) shrimp-like crustaceans. Their heads and thorax are fused to form a carapace, the abdomen is tubular and the uropods are slender and biramous. There are 1500 species worldwide, approximately 50 of which occur on the Pacific coast of the United States (Watling 2007; Gerken and Martin 2014). Cumaceans belong to the Malacostraca, and are characterized by a carapace that covers the first three or four thoracic somites. They also have an anterior extension (pseudolobes), a telson that is present or reduced and fused with the last pleonite, eyes that are united dorsally, a second antenna that is without an exopod and pleopods that are absent in females and can be absent or reduced in males (Watling 2007).

The superorder Peracarida includes cumaceans, mysids, isopods, tanaids and amphipods. Cumaceans can be separated from mysids by their single compound eye (particularly in the males), as mysids have large stalked eyes. Mysids have a carapace which covers the entire thorax, while cumaceans have several posterior segments exposed. Euphausiids belong to the superorder Eucarida (along with decapods) and are pelagic and marine, but might occasionally be found in estuaries. They have biramous thoracic appendages (cumacean pereopods are uniramous, with some thoracic exopodites). Additionally, euphausiids have strong pleopods for

swimming and cumacean pleopods, when present, are small.

The four local cumacean families can be divided into those with a freely articulated telson and those without, the former comprise the Lampropidae and Diastylidae, while the latter comprise the Leuconidae and Nannastacidae (Watling 2007). Cumacean families that lack an articulated telson are consistently monophyletic on molecular phylogenies and are likely derived within the Cumacea (Haye et al. 2004). However, morphological characters used to differentiate cumacean families (e.g. number of pleopods in males) may be homoplasious (see Haye et al. 2004). The Lampropidae have three or more terminal setae on the telson while the Diastylidae have only 0–2. Diastylidae males can have two or zero pairs of pleopods and the Lampropidae can have three or zero. Uropod endopods in diastylids can have two or three articles and in lampropids there are always three.

In the Diastylidae there are five local species in three genera including *Anchicolurus* and *Diastylopsis* (one local species each) and *Diastylis* (three local species) (Watling 2007). The Lampropidae includes six local species in the genera *Hemilamprops* and *Mesolamprops* (each with one local species) and the *Lamprops* (four local species, see *L. quadriplicata*, this guide).

Hemilamprops californiensis occurs from northern California to Vancouver Island (Lie 1969). This genus is noted for its long, slender body and small carapace with a rounded anterolateral edge. *Hemilamprops* species lack the four carapace folds of *L. quadriplicata*, although *H. californica* has one recurved fold on its carapace. *Hemilamprops californiensis* also has three pairs of male pleopods, and 3–4 pairs of lateral telson spines, while *L. quadriplicata* has 0 and 3–5, respectively. *Mesolamprops dillonensis* is characterized by its two pairs of male pleopods (Given 1964), while *Lamprops* males have no pleopods. *Mesolamprops dillonensis* has been found in northern California.

There are several other species of *Lamprops* in the northeastern Pacific including *L. obfuscatus*, *L. triserratus* and *L. tomalesi*. The two former species were previously members of the genus *Diastylis*

(Watling 2007). *Lamprops triserratus* has a carapace with oblique lateral ridges, while *L. obfuscatus* and *L. tomalesi* have carapaces without any ridges. *Lamprops tomalesi* was described from Dillon Beach, California. It has large chromatophores on its carapace, especially in the ovigerous females and the carapace lacks the four oblique folds of *L. quadriplicata*. It has five terminal telson spines, but no lateral ones.

Lamprops quadriplicata is perhaps most similar to the large European *L. fasciatus*, which is also found in Alaska. In fact, the two are so similar previous researchers have thought them synonymous (Zimmer 1980). *Lamprops fasciatus* has only three oblique folds on its carapace, not four. Like *L. quadriplicata*, it has five apical telson spines, but they are unequal in length, the outermost and middle ones being the longest (Smith 1879). In addition, *L. fasciatus* has strong transverse brownish violet pigment bands, from which it derives its name and females can be up to nine mm in length (Sars 1900).

Ecological Information

Range: Type region is along the northeast Atlantic coast (Smith 1879). Range includes the Atlantic coast of North America as well as the Arctic coasts of Alaska and the Pacific coast from Alaska south to Oregon and central California. Range also includes the northwest Pacific including Kamchatka, the Kuriles and Peter the Great Bay (Given 1965).

Local Distribution: Oregon distribution in Coos Bay, Yaquina Bay, and the Columbia River Estuary.

Habitat: Sandy or muddy benthic habitats (Sars 1900). Prefers grains smaller than 200 μm in diameter (Wieser 1956). The abundance, small size and sensitivity make *L. quadriplicata* and other cumaceans the subject of sediment toxicity testing (e.g. Swartz et al. 1979)

Salinity:

Temperature:

Tidal Level: Subtidally, in the Alaskan Arctic from 13–67 m (Given 1965). Mid to outer continental shelf along the Atlantic (Watling 1979) and from +1.4 meters down to -0.8 meters in Puget Sound, Washington (Wieser 1956).

Associates:

Abundance: Most abundant in plankton samples (oblique, night time tows from sea surface to near bottom) in winter and spring months in the Gulf of Maine (Grabe 1996).

Life-History Information

Reproduction: Development in cumaceans is direct, where eggs hatch within a marsupium, and development is thought to be similar among cumacean genera (e.g. *Leucon*, *Lamprops* and *Pseudocuma*, Gerken and Martin 2014). Little is known about the development of *L. quadriplicata*, specifically. In *Manocuma stellifera*, an Atlantic intertidal cumacean, mating occurs at night in plankton (Gnewuch and Croker 1973; Watling 1979), during the short swarming period. Females molt 12–96 hours before oviposition (in the lab). Eggs are probably fertilized as they are released into the marsupium, where they are carried to nauplius larval stage. Some other intertidal species have two breeding generations per year, one in summer and in fall (see Corey 1969, 1976 in Watling 1979).

Larva: Cumacean development proceeds from an egg to two manca stages, a subadult and finally, an adult. The manca stage resembles the adult, but is defined by a lack of the fifth pair of pleopods (see Fig. 41.1F, Gerken and Martin 2014). The mancae of *M. stellifera* molt three times to manca stage and the young leave the marsupium, molt several more times into subadult morphology, with mature gonads and secondary sexual characteristics present (see Corey 1969, 1976 in Watling 1979).

Juvenile:

Longevity:

Growth Rate:

Cumacean growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: In muddy habitats, *L. quadriplicata* feeds on minute suspended particles (Foxon 1936; Kozloff 1993). Feeding occurs when animal is half-buried and sand grains are collected with the first pereopods, mouthparts then scrape off organic matter. The cleaned grains are then tossed away, up over

carapace, burying animal more deeply. This “sand grain rolling” is a continuous process in *L. quadriplicata*, and they are rarely observed doing anything else (Foxon 1936).

Predators:

Behavior: Males often found swimming on the surface (Foxon 1936). Swimming is with thoracic exopodites and by rapid flexing of abdomen. Telson spines may be used to clean mouthparts while animal swims in an upward and curved position. Female *L. fasciatus* can swim at speeds up to 1 m per 90–100 seconds at 12 °C or 1 m per 65–75 seconds at 20 °C. Ovigerous females sink at rates of 1 m per 40 seconds at 12 °C and 1 m per 38 seconds at 20 °C. Non-ovigerous females, on the other hand, sink at rates of 1 m per 55 seconds. Individuals can bury themselves easily, using the three pairs of posterior pereopods (Foxon 1936).

Bibliography

1. FAGE, L. 1951. Cumacés. Faune de France:1-136.
2. FOXON, G. E. H. 1936. Notes on the natural history of certain sand-dwelling Cumacea. *Journal of Natural History Series* 10. 17:377-393.
3. GERKEN, S., and J. W. MARTIN. 2014. Cumacea, p. 216-218. *In: Atlas of crustacean larvae*. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
4. GIVEN, R. R. 1964. The cumacean fauna of the southern California continental shelf: No. 2. the new family Mesolampropidae. *Crustaceana*. 7:284-292.
5. —. 1965. Five collections of Cumacea from Alaskan arctic. *Arctic*. 18:213-&.
6. GNEWUCH, W. T., and R. A. CROKER. 1973. Macrofauna of northern New England marine sand. 1. Biology of *Mancocuma stellifera* (Zimmer, 1943) (Crustacea, Cumacea). *Canadian Journal of Zoology*. 51:1011-1020.
7. GRABE, S. A. 1996. Composition and seasonality of nocturnal peracarid zooplankton from coastal New Hampshire (USA) waters, 1978-1980. *Journal of Plankton Research*. 18:881-894.
8. HART, J. F. L. 1930. Some Cumacea of the Vancouver Island region. *Contributions to Canadian Biology*. 6:23-40.
9. HAYE, P. A., I. KORNFIELD, and L. WATLING. 2004. Molecular insights into Cumacean family relationships (Crustacea, Cumacea). *Molecular Phylogenetics and Evolution*. 30:798-809.
10. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
11. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
12. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
13. LIE, U. 1969. Cumacea from Puget Sound and off the northwestern coast of Washington with descriptions of two new species. *Crustaceana*. 17:19-30.
14. PROCTER, W. 1933. Biological survey of the Mount Desert region. Wistar Institute of Anatomy and Biology, Philadelphia.
15. SARS, G. O. 1900. An account of the crustacea of Norway. III: Cumacea. Bergen Museum, Bergen.
16. SMITH, S. I. 1879. The stalk-eyed crustaceans of the Atlantic coast of North America, north of Cape Cod. *Transactions of the Connecticut Academy of Arts and Sciences*. 5:27-138.
17. SWARTZ, R. C., W. A. DEBEN, and F. A. COLE. 1979. Bioassay for the toxicity of sediment to marine macrobenthos. *Journal Water Pollution Control Federation*. 51:944-950.

18. WATLING, L. 1979. Marine flora and fauna of the northeastern United States: Crustacea, Cumacea. NOAA Technical Report NMFS Circular, Washington.
19. —. 2007. Arthropoda: Cumacea. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley.
20. WIESER, W. 1956. Factors influencing the choice of substratum in *Cumella vulgaris* (Hart) (Crustacea, Cumacea). *Limnology and Oceanography*. 1:274-285.
21. ZIMMER, C. 1980. Cumaceans of the American Atlantic boreal coast region USA (Crustacea, Peracarida). *Smithsonian Contributions to Zoology*:1-29.

Updated 2015

Nippoleucon hinumensis

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Cumacea
Family: Leuconidae

Taxonomy: *Nippoleucon hinumensis* was described as a member of the genus *Hemileucon* at the same time many other cumacean species were described, in the early 1900s. Watling revised the Leuconidae in 1991 and described the first new leuconid genera since 1907. In his manuscript, Watling transferred two *Hemileucon* species (including *H. hinumensis*) to the newly erected genus *Nippoleucon* based on morphological characters (e.g. male antenna two, peduncular articles, Watling 1991) (Lee and Lee 2003).

Description

Size: The illustrated males and females are both 5 mm in length (from the Columbia River Estuary).

Color: Descriptions of color in the Cumacea are difficult as many species were described based on preserved material, where the color fades.

General Morphology: Cumaceans are easily recognizable by a large and inflated carapace and a (relatively) slender, flexible thorax and abdomen (Kozloff 1993; Gerken and Martin 2014). Their bodies can be divided into these three major regions: the **cephalon** (head) that is covered by a **carapace** and includes the first five pairs of appendages (antennae, mandibles, maxillae, collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax), usually consisting of five thoracic somites, followed by the **pleon** (abdomen) with consistently six pleonites. The fifth pleonite is usually the longest and the pleonites are lacking **pleopods** in female individuals. The cumacean family Leuconidae are characterized by the lack of a free telsons and uropod endopods that are biarticulate (Watling 2007). (For general morphology of *N. hinumensis*, see also Plate 229A, Watling 2007.)

Cephalon: A carapace covers the cephalon and first three thoracic somites and is

expanded on either side to form a branchial chamber (Watling 2007).

Carapace: Female carapace with a wide antennal notch that is pronounced into a tooth at an anterolateral angle (Fig. 1). Anterior and posterior edges are slightly serrate and the anterior half of the carina (ridge) is finely and irregularly serrate. (Jones 1963 found two oblique ridges on the carapace sides, which were not observed here.) The carapace in males has an anterolateral edge that is not pronounced into a tooth and no serrations on anterolateral or lower edges (Jones 1963) and no antennal notch (Calman 1907) (Fig. 2).

Rostrum: Two pseudorostral lobes (together called a pseudorostrum), or extensions of the carapace, extend anteriorly but do not fuse in front of the head in cumaceans (Watling 2007). The pseudorostrum in female *N. hinumensis* is abruptly upturned (Fig. 1) and is more horizontal and truncate in males (Fig. 2).

Eyes: None in either sex.

Antennae: Antennae one are non-unique and short in females while antennae two are rudimentary (Jones 1963). In males, the second antenna has a peduncle with five articles and a long flagellum (12 segments) that extends into the second thoracic segment (Calman 1907) (Fig. 3).

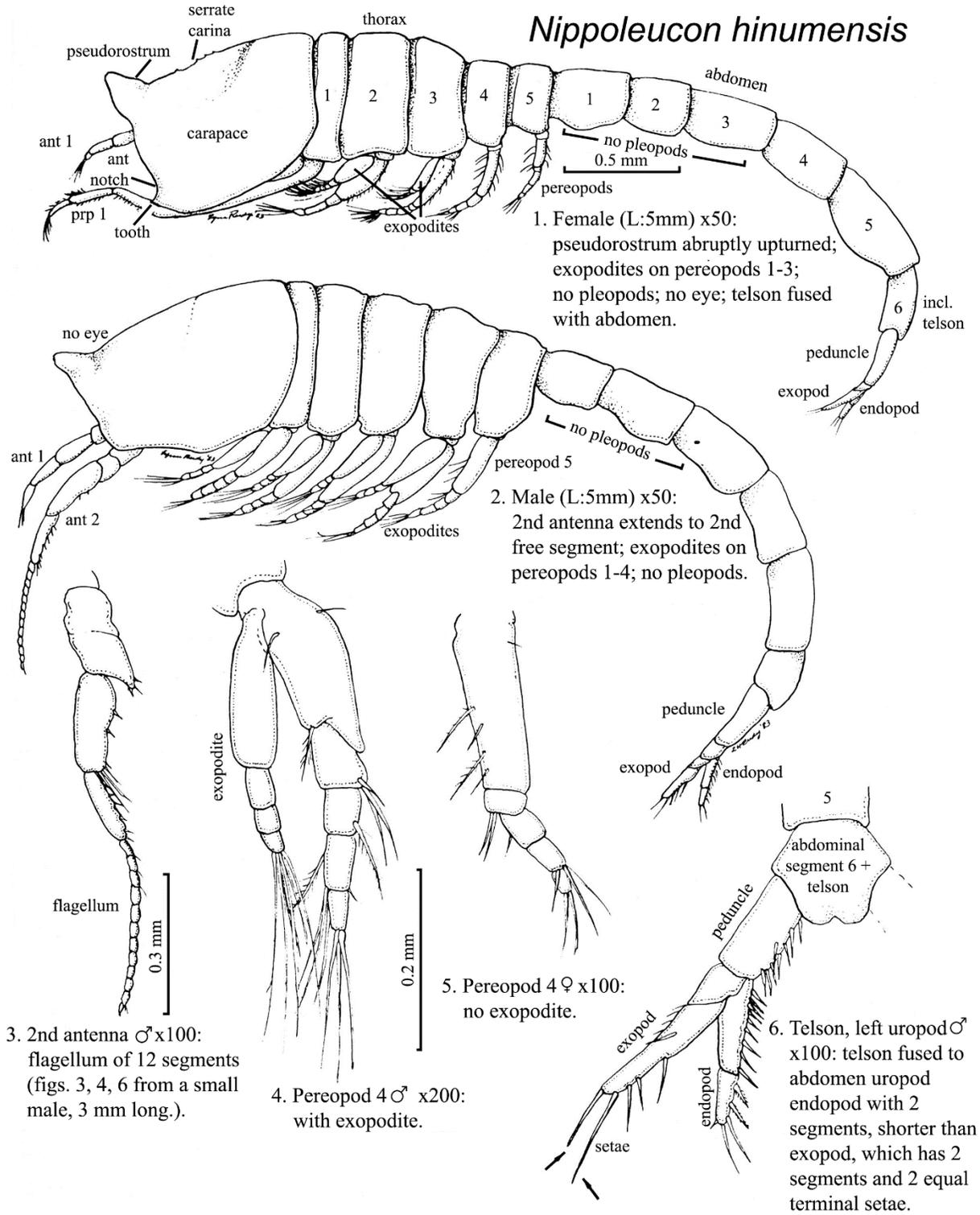
Mouthparts: Two pairs maxillae and three pairs maxillipeds. Mandibles are with massive truncate bases, without palp and with strong molar process, incisor process and lacinia mobilis (Fage 1951) (not figured).

Pereon: Consists of five thoracic somites, each with paired appendages (**pereopods**).

Pereopods: Female pereopod exopodites on somites 1–3 (Leuconidae, Stebbing 1913) (Fig. 1). Pereopods four and five without exopodites (Fig. 5). Male pereopod exopodites on pereopods 1–4, none on five (Calman 1907) (Figs. 2, 4).

Pleon: Consists of six segments and the fifth is longest. The telson is fused with the sixth somite (Figs. 1, 2, 6).

Nippoleucon hinumensis



1. Female (L:5mm) x50:
 pseudorostrum abruptly upturned;
 exopodites on pereopods 1-3;
 no pleopods; no eye; telson fused
 with abdomen.

2. Male (L:5mm) x50:
 2nd antenna extends to 2nd
 free segment; exopodites on
 pereopods 1-4; no pleopods.

3. 2nd antenna ♂ x100:
 flagellum of 12 segments
 (figs. 3, 4, 6 from a small
 male, 3 mm long.).

4. Pereopod 4 ♂ x200:
 with exopodite.

5. Pereopod 4 ♀ x100:
 no exopodite.

6. Telson, left uropod ♂
 x100: telson fused to
 abdomen uropod
 endopod with 2
 segments, shorter than
 exopod, which has 2
 segments and 2 equal
 terminal setae.

Pleopods: All female cumaceans lack pleopods and males in the genus *Nippoleucon* also lack pleopods.

Telson: Telson not independent and fused with last abdominal segment (Leuconidae) (Figs. 6).

Uropods: Uropod peduncles longer than abdominal segment six (Calman 1907) and more than 2/3 as long as the rami (Stebbing 1913). Uropods are slender, cylindrical, and biramous. The endopod inner branch is biarticulate. The first article of the endopod is longer than the second, and is with nine spines on the inner edge. The endopod is shorter than the exopod (Jones 1963) (Fig. 6). The exopod (outer branch) is also biarticulate (as in all Cumacea, Watling 1979), has two unequal terminal setae (Calman 1907; Jones 1963) (Fig. 6), and a series of setae on both inner and outer edges (Calman 1907). The uropods are similar in both sexes.

Sexual Dimorphism: Not as strong in this species as in those in which males have eyes and pleopods. Males are more slender and longer than females. Males also have long second antennae. A brood pouch is present in mature females only and is large, simple and transparent (not figured).

Possible Misidentifications

Cumaceans are very small (range 1 mm–1 cm) shrimp-like crustaceans. Their heads and thorax are fused to form a carapace, the abdomen is tubular and the uropods are slender and biramous. There are 1500 species worldwide, approximately 50 of which occur on the Pacific coast of the United States (Watling 2007; Gerken and Martin 2014). Cumaceans belong to the Malacostraca, and are characterized by a carapace that covers the first three or four thoracic somites and has an anterior extension (pseudolobes), a telson that is present or reduced and fused with the last pleonite, eyes that are united dorsally, a second antenna that is without an exopod and pleopods that are absent in females and can be absent or reduced in males (Watling 2007).

The superorder Peracarida includes cumaceans, mysids, isopods, tanaids and amphipods. Cumaceans can be separated from mysids by their single compound eye (particularly in the males), as mysids have

large stalked eyes. Mysids have a carapace which covers the entire thorax, while cumaceans have several posterior segments exposed. Euphausiids belong to the superorder Eucarida (along with decapods) and are pelagic and marine, but might occasionally be found in estuaries. They have biramous thoracic appendages (cumacean pereopods are uniramous, with some thoracic exopodites). Additionally, euphausiids have strong pleopods for swimming and cumacean pleopods, when present, are small.

The four local cumacean families can be divided into those with a freely articulated telson and those without, the former comprise the Lampropidae (see *Lamprops quadriplicata*, this guide) and Diastylidae, while the latter comprise the Leuconidae and Nannastacidae (see *Cumella vulgaris*, this guide) (Watling 2007). Cumacean families that lack an articulated telson are consistently monophyletic on molecular phylogenies and are likely derived within the Cumacea (Haye et al. 2004). However, morphological characters used to differentiate cumacean families (e.g. number of pleopods in males) may be homoplasious (see Haye et al. 2004).

The Leuconidae (like the Nannastacidae) lack the independent telson. However, they always have a biarticulate uropod endopod, not a uniramous one as in Nannastacidae. Members of the Leuconidae often have up to two pairs of male pleopods (there are none in Nannastacidae) and have exopodites on all five pairs of pereopods (rarely on three). Leuconid females have exopodites on four (rarely on three) pairs of pereopods (Watling 1979). Numbers of pereopodal exopodites in both sexes are too alike in the families Leuconidae and Nannastacidae and may not serve as dependable characters for identification. One of the oldest cumacean families (Watling 1991), the Leuconidae were recently been removed from the Hemileuconidae (Given 1969). (This separation is not followed by Jones 1963, however, see below.) Both families lack an independent telson and both have a biarticulate endopod on the uropod. In Leuconidae, however, there are usually two pairs of male pleopods, rarely 1 or 0 pairs, while there are no male pleopods in the

Hemileuconidae. Leuconid males have five (rarely three) pereopods with exopodites. Hemileuconid males, on the other hand, have four pairs of pereopodal exopodites. Male Leuconidae have second antennae that are as long as the body, but they are shorter in the Hemileuconidae (Given 1969). Female Leuconidae have four (rarely three) pairs of thoracic exopodites, while there are three pairs in the Hemileuconidae. Thus, it might be difficult separating females of these two families.

Two genera, *Eudorella* and *Nippoleucon*, each with a single species, are currently reported from central California to Oregon (Watling 2007). *Eudorella pacifica* has a truncate edge to the carapace, like *N. hinumensis*. *Eudorella pacifica* females, however, have a uropod exopod that is shorter than the endopod.

The family Nannastacidae lack an independent telson, the males have no pleopods and the endopod of the uropod is unarticulate. The Lampropidae and Diastylidae have a freely articulated telson and the former family has three or more terminal setae on the telson while the latter has 0–2. The Lampropidae includes six local species in the genera *Hemilamprops* and *Mesolamprops* (each with one local species) and the *Lamprops* (four local species, see *L. quadriplicata*, this guide). In the Diastylidae there are five local species in three genera including *Anchicolurus* and *Diastylopsis* (one local species each) and *Diastylis* (three local species) (Watling 2007).

Ecological Information

Range: Type locality is New Zealand, but this species was introduced to west coast estuaries (e.g. San Francisco and Coos bays) from Japan in ballast water (Castillo et al. 2000; Watling 2007).

Local Distribution: Oregon distribution includes the Columbia River Estuary and sites in Coos Bay, such as the North Bend Airport site and South Slough.

Habitat: In sediment during the day and becoming planktonic at night.

Salinity:

Temperature:

Tidal Level:

Associates: Occurs with the cumacean, *Cumella vulgaris*, where individuals are found

at up to 5,600 individuals per square meter in South Slough of Coos Bay (M. Posey, OIMB, unpublished data.)

Abundance: Most common species found in Columbia River estuary (R. Emmett, NOAA, Astoria, personal communication).

Life-History Information

Reproduction: Development in cumaceans is direct, where eggs hatch within a marsupium, and development is thought to be similar among cumacean genera (e.g. *Leucon*, *Lamprops* and *Pseudocuma*, Gerken and Martin 2014). The life-history of *N. hinumensis* was documented by Akiyama and Yamamoto in 2004 from individuals collected from Seto, Japan. In that region, ovigerous females are 1.2 times larger than males and begin to incubate their first brood (containing 57 larvae) in February, often incubating a second brood (containing 42 larvae) until late April. In *Manocuma stellifera*, an Atlantic intertidal cumacean, mating occurs at night in plankton (Gnewuch and Croker 1973; Watling 1979), during the short swarming period. Females molt 12–96 hours before oviposition (in the lab). Eggs are probably fertilized as they are released into the marsupium, where they are carried to nauplius larval stage. Some other intertidal species have two breeding generations per year, one in summer and in fall (see Corey 1969, 1976 in Watling 1979).

Larva: Cumacean development proceeds from an egg to two manca stages, a subadult and finally, an adult. The manca stage resembles the adult, but is defined by a lack of the fifth pair of pleopods (see Fig. 41.1F, Gerken and Martin 2014). In *N. hinumensis*, manca larvae are released and most recruitment takes place in April. Post-marsupial individuals undergo eight in-stars in males and nine in females, with 10 days between molts in the first four in-stars and two weeks thereafter (when not in diapause) (Akiyama and Yamamoto 2004a). The mancae of *M. stellifera* molt three times and the young leave the marsupium, molt several more times into subadult morphology, with mature gonads and secondary sexual characteristics present (see Corey 1969, 1976 in Watling 1979).

Juvenile:

Longevity: The life-span of many cold water leuconid cumaceans is on the order of a few years. In Seto, Japan, population generation times occur on an annual cycle and the life-span can be divided into three phases (see **growth rate**) (Akiyama and Yamamoto 2004a).

Growth Rate:

Cumacean growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007). In *N. hinumensis*, growth can be divided into three phases: early growth from April to May, no growth (or diapause) from May to November and a later growth phase from December to March (Akiyama and Yamamoto 2004a). This summer period of diapause or arrested growth is unique to this species and, interestingly, not all populations undergo a diapause phase (see Akiyama and Yamamoto 2004b).

Food: Filters small particles from below sediment surface or grazes on surface grains (Watling 1979; Kozloff 1993).

Predators:

Behavior:

Bibliography

1. AKIYAMA, T., and M. YAMAMOTO. 2004a. Life history of *Nippoleucon hinumensis* (Crustacea: Cumacea: Leuconidae) in Seto Inland Sea of Japan. I. Summer diapause and molt cycle. *Marine Ecology Progress Series*. 284:211-225.
2. —. 2004b. Life history of *Nippoleucon hinumensis* (Crustacea: Cumacea: Leuconidae) in Seto Inland Sea of Japan. II. Non-diapausing subpopulation. *Marine Ecology Progress Series*. 284:227-235.
3. CALMAN, W. T. 1907. On new or rare crustacea of the order Cumacea from the collection of the Copenhagen Museum Part I, The families Bodotriidae, Vauntomponiidae, and Leuconidae. *The Transactions of the Zoological Society of London*. 18:1-42.
4. CASTILLO, G. C., H. W. LI, and P. A. ROSSIGNOL. 2000. Absence of overall feedback in a benthic estuarine community: A system potentially buffered from impacts of biological invasions. *Estuaries*. 23:275-291.
5. FAGE, L. 1951. Cumacés. *Faune de France*:1-136.
6. GERKEN, S., and J. W. MARTIN. 2014. Cumacea, p. 216-218. *In: Atlas of crustacean larvae*. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
7. GIVEN, R. R. 1969. The Cumacean fauna of the Southern California continental shelf. No. 1, Family Leuconidae. *Bulletin, Southern California Academy of Sciences*. 60:129-146.
8. GNEWUCH, W. T., and R. A. CROKER. 1973. Macrofauna of northern New England marine sand. 1. Biology of *Mancocuma stellifera* (Zimmer, 1943) (Crustacea, Cumacea). *Canadian Journal of Zoology*. 51:1011-1020.
9. HAYE, P. A., I. KORNFIELD, and L. WATLING. 2004. Molecular insights into Cumacean family relationships (Crustacea, Cumacea). *Molecular Phylogenetics and Evolution*. 30:798-809.
10. JONES, N. S. 1963. The marine fauna of New Zealand: Crustaceans of the order Cumacea. *Bulletin of the New Zealand Department of Scientific and Industrial Research*. No. 152:1-81.
11. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
12. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
13. LEE, C., and K. LEE. 2003. A new record of genus *Nippoleucon* (Cumacea: Leuconidae) from Korea.

- Korean Journal of Systematic Zoology.
19:257-265.
14. STEBBING, T. R. 1913. Crustacea, Cumacea (Sympoda) Das Tierreich. 39:152-153.
 15. WATLING, L. 1979. Marine flora and fauna of the northeastern United States: Crustacea, Cumacea. NOAA Technical Report NMFS Circular, Washington.
 16. —. 1991. Revision of the Cumacean family Leuconidae. Journal of Crustacean Biology. 11:569-582.
 17. —. 2007. Arthropoda: Cumacea. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley.

Updated 2015

Cumella vulgaris

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Cumacea
Family: Nannastacidae

Description

Size: In the original description by Hart (1930) from Vancouver Island, an ovigerous female was 2.5 mm in length and a male, 3.0 mm long (Hart 1930). The illustrated specimens (from Coos Bay) include a female, 2.5 mm long, and a young male, 2.1 mm in length. *Cumella vulgaris* is one of the smallest cumacean species (Sars 1900).

Color: Males are dark brown except for lighter distal segments and appendages. The female carapace and sixth pleonite are dark brown and the rest of the body is light brown or white (Gonor et al. 1979).

General Morphology: Cumaceans are easily recognizable by a large and inflated carapace and a (relatively) slender, flexible thorax and abdomen (Kozloff 1993; Gerken and Martin 2014) (Fig. 1). Their bodies can be divided into these three major regions: the **cephalon** (head) that is covered by a **carapace** and includes the first five pairs of appendages (antennae, mandibles, maxillae, collectively the **mouthparts**). Posterior to the cephalon is the **pereon** (thorax), usually consisting of five thoracic somites, followed by the **pleon** (abdomen) with consistently six pleonites. The fifth pleonite is usually the longest and the pleonites are lacking **pleopods** in female individuals. The cumacean family Nannastacidae are characterized by the lack of a free telsons and uropod endopods that are uniarticulate (Watling 2007). (For general morphology of *C. vulgaris*, see also Plate 229B, Watling 2007.)

Cephalon: A carapace covers the cephalon and first three thoracic somites and is expanded on either side to form a branchial chamber (Watling 2007).

Carapace: Female carapace is large and deep, with a smooth mid-dorsal carina (ridge) with a depression on each side (on posterior margin). A deep antennal notch is present, with an acute antero-lateral angle (Fig. 1). The male carapace is slender, the

antennal notch is not as deep as in females, and the dorsal carina is almost absent (Fig. 3).

Rostrum: Two pseudorostral lobes (together called a pseudorostrum), or extensions of the carapace, extend anteriorly but do not fuse in front of the head in cumaceans (Watling 2007). The pseudorostrum in female *C. vulgaris* is relatively short, minutely serrate anteriorly and strongly pronounced (Fig. 1). In males, the pseudorostral projection is shorter (Sars 1900) (Fig. 3).

Eyes: Conspicuous and circular in females (Gonor et al. 1979) (Fig. 1). In males a single central sessile eye, with seven equal lenses, is more prominent (Gonor et al. 1979) (Fig. 4).

Antennae: Female antennule is rather stout, not easily visible, and with rudimentary inner flagellum (Nannastacidae, Fage 1951). The second antenna in females is with two large plumose setae (Hart 1930) (not figured).

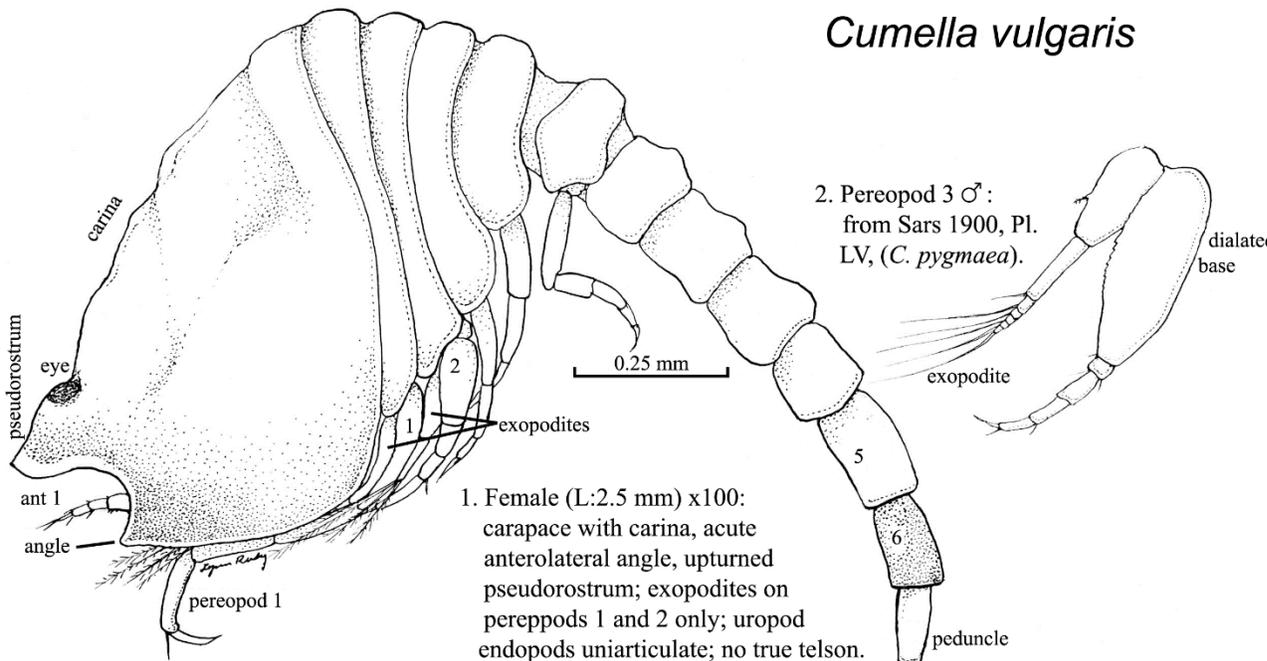
Mouthparts: Mandibles are not unique and the bases are not massive (Fage 1951) (not figured).

Pereon: Consists of five thoracic somites, each with paired appendages (**pereopods**) (Figs. 1–3).

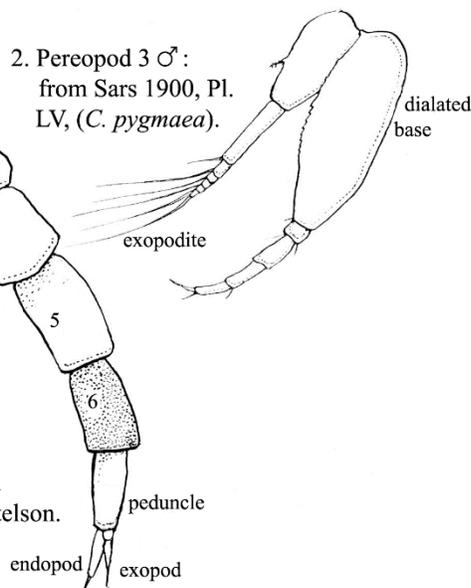
Pereopods: The first pereopods in females are with bases serrate on the outer distal margin. The dactyl and propodus are equal to the carpus in length. The second pereopods are stout, and the dactyl is twice as long as the propodus. The exopodites are present on the first two pairs of pereopods only (*Cumella*, Lie 1969). The last three pereopods are stout (Fig. 1). The first four pereopod bases in males are more dilated than in females and exopodites are present on the first four pereopods (absent on fifth) (Figs. 2, 3).

Pleon: Long and narrow in males and stouter in females. Consists of six articles or pleonites, and lacking pleopods (Figs. 1, 3).

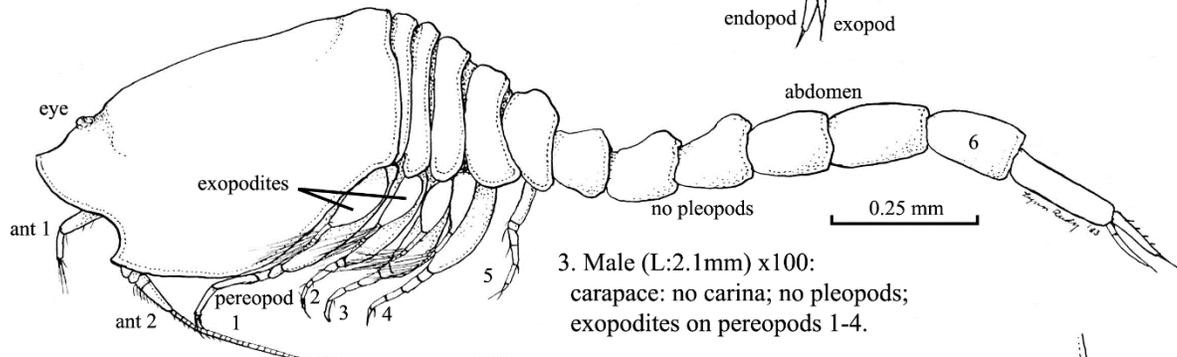
Cumella vulgaris



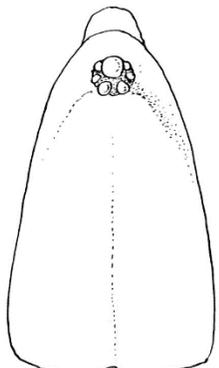
1. Female (L:2.5 mm) x100:
carapace with carina, acute anterolateral angle, upturned pseudorostrum; exopodites on pereopods 1 and 2 only; uropod endopods uniarticulate; no true telson.



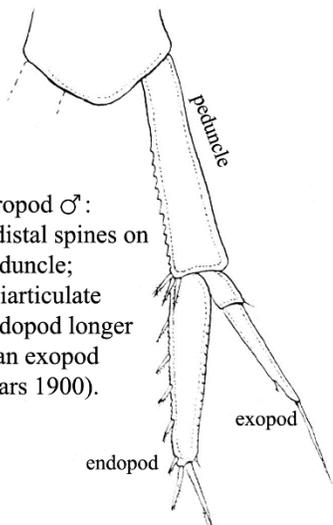
2. Pereopod 3 ♂:
from Sars 1900, Pl. LV, (*C. pygmaea*).



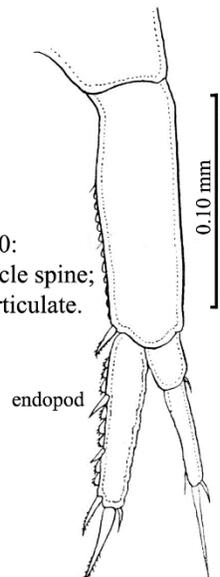
3. Male (L:2.1mm) x100:
carapace: no carina; no pleopods;
exopodites on pereopods 1-4.



4. Carapace (dorsal view) ♂ x100:
7 lensed eye; no carina.



5. Uropod ♂:
3 distal spines on peduncle;
uniarticulate endopod longer than exopod (Sars 1900).



6. Uropod ♀ x350:
1 distal peduncle spine;
endopod uniarticulate.

Pleopods: All female cumaceans lack pleopods (Fig.1) and males in the family Nannastacidae also lack pleopods (Watling 2007) (Fig. 3).

Telson: Telson short, not freely articulated and fused to sixth abdominal article (Nannastacidae, Watling 2007) (Figs. 1, 3).

Uropods: The uropod peduncles in females have inner margin with only one spine on the inner distal angle (Gonor et al. 1979) (Fig. 6). The uropod endopod is uniarticulate (compare to biarticulate endopod in *Nippoleucon hinumensis*), larger than exopod, denticulate on inner margin, with two stout spines, and one strong apical spine. The exopod is with two articles (as in all cumaceans), is ½ the width of the endopod, and with one slender apical spine (Fig. 6) (Gonor et al. 1979). The uropods of males are slim and the peduncle is denticulate, longer than rami (Fage 1951), and with three distal spines. The endopod is with only a single article (Nannastacidae, Watling 1979), while the exopod is with two articles (Fig. 5).

Sexual Dimorphism: Quite strong sexual dimorphism is observed in *C. vulgaris*. Females are generally shorter and stouter than males and mature individuals have a brood pouch. The female eye lacks the obvious large lenses found in males (Fig. 4). Female specimens have a broader carapace and uropods, a strong carapace carina, and exopodites that appear only on the first two pairs of pereopods. Males have a compound eye, are slim, lack a strong carapace carina and have a very long second antenna. Males also have four pereopod exopodites and some uropod distinctions.

Possible Misidentifications

Cumaceans are very small (range 1 mm–1 cm) shrimp-like crustaceans. Their heads and thorax are fused to form a carapace, the abdomen is tubular and the uropods are slender and biramous. There are 1500 species worldwide, approximately 50 of which occur on the Pacific coast of the United States (Watling 2007; Gerken and Martin 2014). Cumaceans belong to the Malacostraca, and are characterized by a carapace that covers the first three or four thoracic somites. They also have an anterior extension (pseudolobes), a telson that is present or reduced and fused with the last

pleonite, eyes that are united dorsally, a second antenna that is without an exopod and pleopods that are absent in females and can be absent or reduced in males (Watling 2007).

The superorder Peracarida includes cumaceans, mysids, isopods, tanaids and amphipods. Cumaceans can be separated from mysids by their single compound eye (particularly in the males), as mysids have large stalked eyes. Mysids have a carapace which covers the entire thorax, while cumaceans have several posterior segments exposed (e.g. Figs. 1, 3). Euphausiids belong to the superorder Eucarida (along with decapods) and are pelagic and marine, but might occasionally be found in estuaries. They have biramous thoracic appendages (cumacean pereopods are uniramous, with some thoracic exopodites). Additionally, euphausiids have strong pleopods for swimming and cumacean pleopods, when present, are small.

The four local cumacean families can be divided into those with a freely articulated telson and those without, the former comprise the Lampropidae and Diastylidae, while the latter comprise the Leuconidae and Nannastacidae (Watling 2007). Cumacean families that lack an articulated telson are consistently monophyletic on molecular phylogenies and are likely derived within the Cumacea (Haye et al. 2004). However, morphological characters used to differentiate cumacean families (e.g. number of pleopods in males) may be homoplasious (see Haye et al. 2004).

The family Nannastacidae, in which *Cumella* occurs, lack an independent telson, the males have no pleopods and the endopod of the uropod is uniarticulate. Pereopodal exopodites in the Nannastacidae are as follows: males have five (rarely four or three) pairs and females have three (rarely four or zero) pairs (Watling 1979). *Cumella vulgaris* is the only species in this genus locally. However, *C. pygmaea*, the European species is very like *C. vulgaris* in color and size. The female of *C. pygmaea* is stouter than *C. vulgaris*, with a less inflated carapace and with a dentate crest on the carina. The male of *C. pygmaea* is similar to that of *C. vulgaris*, except that its pedigerous segments are more uneven (Hart 1930). The only other genus of

Nannastacidae from our area is *Campylaspis*. In this genus, both males and females have exopodites only on the first pair of pereopods (Lie 1969). The females have a bulbous carapace with rounded anterolateral angles, unlike *Cumella*, which has an un-inflated carapace and an acute anterolateral angles. *Campylaspis* species have a carapace that extends posteriorly and overhangs the first few pereonites. *Campylaspis canaliculata* has a smooth carapace and females with a marginal anterior-posterior groove. *Campylaspis hartae* has a carapace with large ridges, but no bumps, and *C. rubromaculata* has a carapace with a series of bumps or tubercles and shallow ridges (Watling 2007).

The Leuconidae (like the Nannastacidae) lack an independent telson. However, they always have a biarticulate uropod endopod, not a uniramous one as in Nannastacidae. Members of the Leuconidae often have up to two pairs of male pleopods (there are none in Nannastacidae) and leuconid males have exopodites on all five pairs of pereopods (rarely on three). Leuconid females have exopodites on four (rarely on three) pairs of pereopods (Watling 1979). Thus, numbers of pereopodal exopodites in both sexes are too alike in the families Leuconidae and Nannastacidae to serve as dependable determining characters. Of the Leuconidae, the genera *Eudorella*, and *Nippoleucon* (see *N. hinumensis*, this guide) occur on the Pacific Coast (each with one local species).

The Lampropidae and Diastylidae have a freely articulated telsons and the former family has three or more terminal setae on the telson while the latter has 0–2. The Lampropidae includes six local species in the genera *Hemilamprops* and *Mesolamprops* (each with one local species) and the *Lamprops* (four local species, see *L. quadriplicata*, this guide). In the Diastylidae there are five local species in three genera including *Anchicolurus* and *Diastylopsis* (one local species each) and *Diastylis* (three local species) (Watling 2007).

Ecological Information

Range: Type locality is Puget Sound (Hart 1930), known range from central California to Oregon (Watling 2007).

Local Distribution: Known to occur in Coos and Yaquina bays.

Habitat: Cumacean species choose substrates mostly based on food availability. *Cumella vulgaris* prefers fine sand (grains with diameter less than 160 μm) and dislikes dry sand (in lab experiments). Males can be found in sand with grains of 200 μm diameter and smaller (Wieser 1956) and are also found on the water surface, near shore (Hart 1930). *Cumella vulgaris* actively avoids habitats with fast currents (McCauley et al. 1977). Applications of the insecticide Sevin caused significant decreases (90%) in *C. vulgaris* abundance (Simenstad and Cordell 1989).

Salinity: Collected at salinities of 30 (in Coos Bay).

Temperature:

Tidal Level: Intertidal and usually found below +1.5 meters MLLW down to -0.6 meters (Wieser 1956). Individuals found on water surface and in standing water at low tide (Hart 1930). Subtidal populations are reported as deep as 10 m (Jones 1961).

Associates:

Abundance: The most common cumacean in Puget Sound and San Juan Islands, Washington (Wieser 1956) and a common intertidal species in central California. In Coos Bay, it was the second most abundant crustacean (by numbers) found in a North Bend study site (Gonor et al. 1979). With *Nippoleucon hinumensis*, it was found at up to 5,600 individuals per square meter in South Slough of Coos Bay (personal communication, M. Posey, OIMB). In Willapa Bay, *C. vulgaris* was the third most abundant organism in *Neotrypaea* beds, ninth most abundant in *Zostera* beds, seventh most abundant in oyster beds and twelfth most abundant in bare mud and sand (Ferraro and Cole 2007).

Life-History Information

Reproduction: Development in cumaceans is direct, where eggs hatch within a marsupium, and development is thought to be similar among cumacean genera (e.g. *Leucon*, *Lamprops* and *Pseudocuma*, Gerken and Martin 2014). Little is known about the development of *C. vulgaris*, specifically. In *Manocuma stellifera*, an Atlantic intertidal cumacean, mating occurs at night in plankton (Gnewuch and Croker 1973; Watling 1979),

during the short swarming period. Females molt 12–96 hours before oviposition (in the lab). Eggs are probably fertilized as they are released into the marsupium, where they are carried to a manca stage. Some other intertidal species have two breeding generations per year, one in summer and in fall (see Corey 1969, 1976 in Watling 1979).

Larva: Cumacean development proceeds from an egg to two manca stages, a subadult and, finally, an adult. The manca stage resembles the adult, but is defined by a lack of the fifth pair of pleopods (see Fig. 41.1F, Gerken and Martin 2014). The mancae of *M. stellifera* molt three times and the young leave the marsupium, molt several more times into subadult morphology, with mature gonads and secondary sexual characteristics present (see Corey 1969, 1976 in Watling 1979).

Juvenile:

Longevity: In Atlantic intertidal cumaceans, longevity varies with reproductive time of year: an early summer generation may live five months, while late summer and fall broods will overwinter and live 12 and nine months, respectively (see Corey in Watling 1979).

Growth Rate:

Cumacean growth occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007).

Food: A deposit feeder in fine sand and mud. In coarse sand (>150 μm), it is an epistrate feeder that scrapes food off individual grains (Watling 1979; Kozloff 1993). Cumaceans feed while buried and swim to new site when one site has been exploited. *Cumella vulgaris* aggregates to feed (Watling 1979).

Predators: *Cumella vulgaris* have been observed in gut contents of the three-spined sticklebacks (*Gasterosteus aculeatus*) and Northern anchovies (*Engraulis mordax*) (Rasmuson and Morgan 2013). The introduced European green crab (*Carcinus maenas*) significantly reduced *C. vulgaris* populations (Grosholz and Ruiz 1995). Shorebirds feed on *C. vulgaris*, but have no notable impact on abundance (Wilson 1991).

Behavior: Females and juveniles are capable of swimming at speeds of 0.25 to 1.5 cm per second, while males are capable of higher swimming speeds ($\sim 5 \text{ cm s}^{-1}$, King 1977).

Bibliography

1. FAGE, L. 1951. Cumacés. Faune de France:1-136.
2. FERRARO, S. P., and F. A. COLE. 2007. Benthic macrofauna-habitat associations in Willapa Bay, Washington, USA. Estuarine Coastal and Shelf Science. 71:491-507.
3. GERKEN, S., and J. W. MARTIN. 2014. Cumacea, p. 216-218. In: Atlas of crustacean larvae. J. W. Martin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore, MD.
4. GNEWUCH, W. T., and R. A. CROKER. 1973. Macrofauna of northern New England marine sand. 1. Biology of *Mancocuma stellifera* (Zimmer, 1943) (Crustacea, Cumacea). Canadian Journal of Zoology. 51:1011-1020.
5. GONOR, J. J., D. R. STREHLOW, and G. E. JOHNSON. 1979. Ecological assessments at the North Bend airport extension site. School of Oceanography, Oregon State University, Salem, OR.
6. GROSHOLZ, E. D., and G. M. RUIZ. 1995. Spread and potential impact of the recently introduced green crab, *Carcinus maenas*, in central California. Marine Biology. 122:239-247.
7. HART, J. F. L. 1930. Some Cumacea of the Vancouver Island region. Contributions to Canadian Biology. 6:23-40.
8. HAYE, P. A., I. KORNFIELD, and L. WATLING. 2004. Molecular insights into Cumacean family relationships (Crustacea, Cumacea). Molecular Phylogenetics and Evolution. 30:798-809.
9. JONES, M. L. 1961. A quantitative evaluation of the benthic fauna off Point Richmond, California. University

- of California Publications in Zoology. 67:219-320.
10. KING, A. R. 1977. Acute effects of sedimentation on *Cumella vulgaris* Hart 1930 (Cumacea). Thesis (M.S.)-- Oregon State University, 1977.
 11. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 12. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 13. LIE, U. 1969. Cumacea from Puget Sound and off the northwestern coast of Washington with descriptions of two new species. *Crustaceana*. 17:19-30.
 14. MCCAULEY, J. E., R. A. PARR, and D. R. HANCOCK. 1977. Benthic infauna and maintenance dredging: case study. *Water Research*. 11:233-242.
 15. RASMUSON, L. K., and S. G. MORGAN. 2013. Fish predation after weakly synchronized larval release in a coastal upwelling system. *Marine Ecology Progress Series*. 490:185-198.
 16. SARS, G. O. 1900. An account of the crustacea of Norway. III: Cumacea. Bergen Museum.
 17. SIMENSTAD, C. A., and J. R. CORDELL. 1989. Effects of Sevin application on littoral flat meiofauna: preliminary sampling in Willapa Bay, June-July 1988. Seattle, Wash. : Fisheries Research Institute, University of Washington School of Fisheries, Seattle, Wash.
 18. WATLING, L. 1979. Marine flora and fauna of the northeastern United States: Crustacea, Cumacea. *In*: NOAA Technical Report NMFS Circular. Dept. of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service ;, Washington.

Updated 2015

Hiebert, T.C. and L. Rasmuson

Mesidotea entomon

A large idoteid isopod

Phylum: Anthropoda, Crustacea
Class: Malacostraca
Order: Isopoda,
Family: Chaetiliidae

Taxonomy: There is confusion regarding the proper genus name for this species (*Mesidotea entomon* or *Saduria entomon*, see International Commission of Zoological Nomenclature (ICZN) 1963, 1964; Rafi and Laubitz 1990). *Mesidotea* was described by Richardson in 1905 but *Saduria*, described by Adams in 1852, is the oldest available name and was determined to be the appropriate name by the ICZN (1964), while *Mesidotea* was listed as an unaccepted junior synonym. However, many authors still recognize Richardson's genus or indicate both names, including the most recent intertidal guide for the northeastern Pacific, which we follow with *M. entomon* (Brusca et al. 2007). Readers should note, however, that use of *Saduria entomon* is just as common and may replace *M. entomon* in the near future.

Description

Size: One of the largest crustaceans in the Baltic Sea and large size is typical of this genus (Richardson 1905). Northwest specimens about 40 mm in length (Hatch 1947). The illustrated specimen, a young mature male from the Columbia River estuary, was 43 mm in length (Fig. 1). Arctic males can be to 95 mm (11 grams) and females 79 (7 grams) mm (McCrimmon and Bray 1962).

Color: Light brown, mottled and with small black chromatophores.

General Morphology: Isopod bodies are dorso-ventrally flattened and can be divided into a compact **cephalon**, with eyes, two **antennae** and **mouthparts**, and a **pereon** (thorax) with eight segments, each bearing similar **pereopods** (hence the name "isopod"). Posterior to the pereon is the **pleon**, or abdomen, with six segments, the last of which is fused with the telson (the **pleotelson**) (see Plate 231, Brusca et al. 2007). The Isopoda can be divided into two groups: ancestral ("short-tailed") groups (i.e. suborders) that have short telsons and derived ("long-tailed") groups with long telsons. Valviferan

(including the Chaetiliidae) isopods have an elongated telson (Figs. 1, 4) (Fig. 73, Ricketts and Calvin 1952). *Mesidotea entomon* individuals are ovate, flattened with broad anterior, tapering to a narrow posterior extremity (Richardson 1905).

Cephalon: Anterior deeply excavate, lateral margins notched into two sub-lobes (Schultz 1969). The anterior lobe is rounded, while the posterior is acute and does not extend beyond the anterior one (Fig. 1) (Richardson 1905). First thoracic segment fused with head (Isopoda, Brusca et al. 2007).

Rostrum:

Eyes: Dorsal eyes are small, round, distinct, compound (Richardson 1905) and set at base of lateral cleft of head (Fig. 1).

Antenna 1: Small and with four articles. The basal article is enlarged and twice as wide as article two. In length, the first antenna reaches the fourth peduncle article of the second antenna (Fig. 1).

Antenna 2: The second antenna is with multiarticulate flagellum (Richardson 1905) and the peduncle consists of five articles, the fifth being longest and the first flagellum article is also quite long.

Mouthparts: Well developed for chewing and biting (Idoteidae, Schultz 1969). Maxilliped palp with five articles (Schultz 1969) (Fig.2) and mandible with molar process and without palp (not figured).

Pereon: Body elongate and depressed with thorax composed of seven segments (Fig. 1) (Brusca et al. 2007).

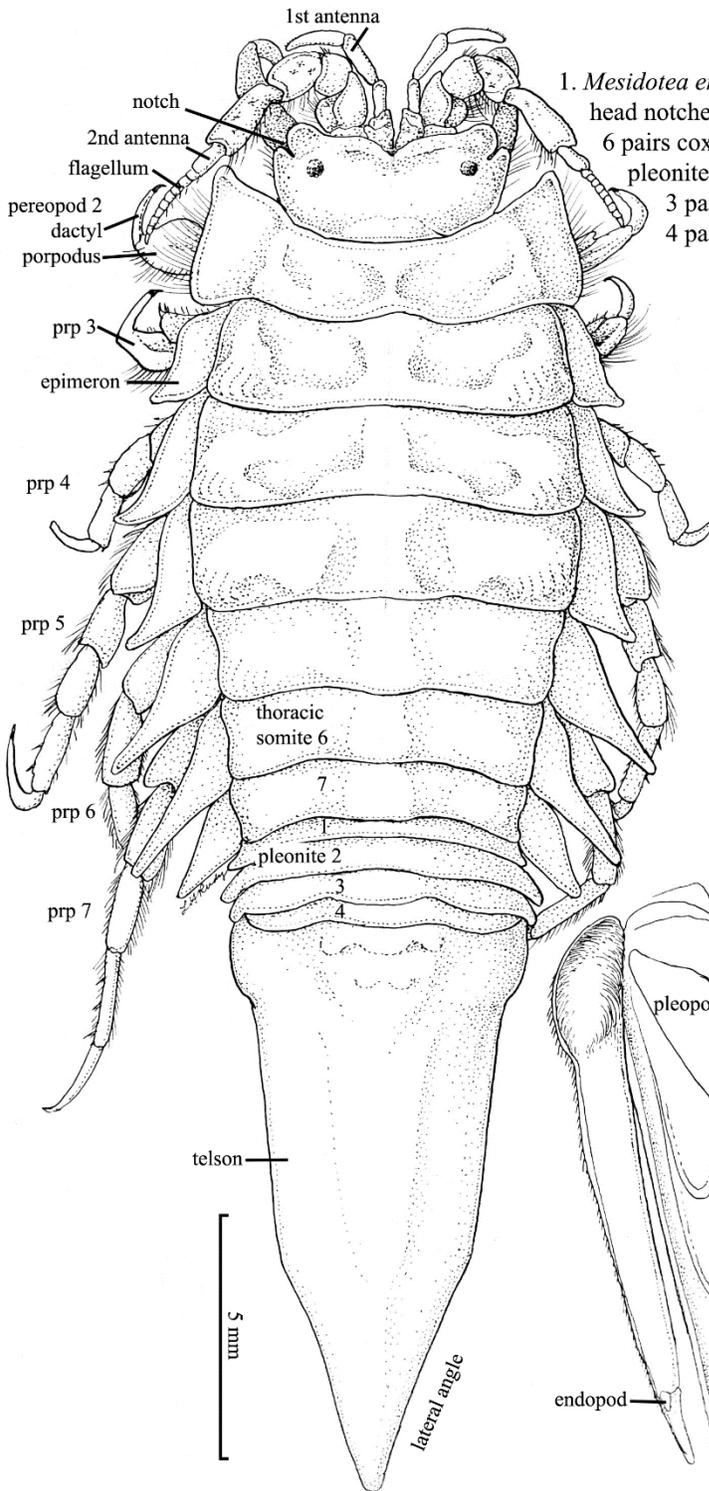
Pereonites: Pereon with seven segments that are all free, subequal and sculptured (Idoteidae, Miller 1975). Distinct coxal epimeral sutures are present on somites 2–7 (Fig. 1), forming long points (epimeron six longest, Richardson 1905).

Pereopods:

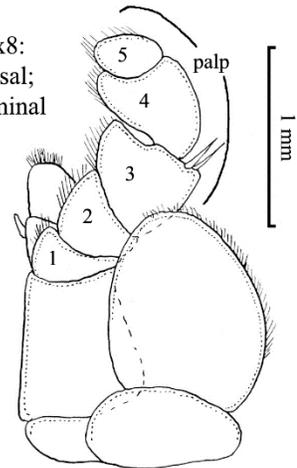
Pleon: Short pleon with five pleonites (Brusca et al. 2007).

Pleonites: Five pleonites, with anterior four short and a long telson, which is partly fused with fourth pleonite (Fig. 1).

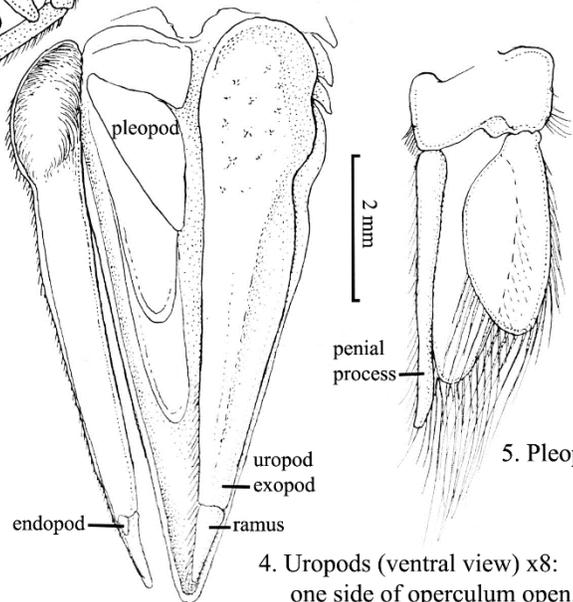
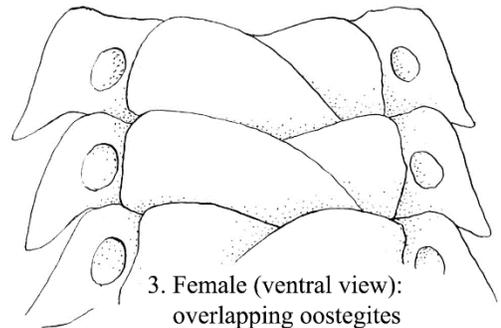
Mesidotea entomon



1. *Mesidotea entomon* (L: 28mm) x8:
head notched laterally; eyes dorsal;
6 pairs coxal epimera; 4 abdominal
pleonites, shield-like telson;
3 pairs prehensile legs,
4 pairs ambulatory.



2. Maxilliped x30:
5 articulated palp.



5. Pleopod 2♂ x12.

4. Uropods (ventral view) x8:
one side of operculum open.

Pleopods: Appendages of the pleon include five respiratory pairs and a single pair of uropods (Brusca et al. 2007). Pleopods are enclosed within operculum (Fig. 4). Male second pleopods with penial process along midline, about 2½ times total pleopod length (McCrimmon and Bray 1962) (nearly mature male, Fig. 5).

Uropods: Ventral. Exopod (outer branch) forms operculum over pleopods (Fig. 4) (Valvifera, Miller 1975), is large, and with two parts – a large upper and a small terminal ramus. The endopod (inner branch) is minute (Schultz 1969) (Fig. 4).

Pleotelson: Long, shield-like, pointed and with lateral angles on posterior 1/3 (Fig.1) and operculum is clearly visible ventrally (Fig.4).

Sexual Dimorphism: Conspicuous sexual dimorphism is rare among isopods, but mature males are considerably larger (130–140% larger) than females in *M. entomon* (Korczyński 1991). Males have a penial process on pleopod two and modified first pleopods, called gonopods (Sadro 2001; Boyko and Wolff 2014). Females have leaf-like overlapping abdominal oostegites (Fig. 3) comprising a thoracic marsupium. This conspicuous brood pouch is lost once young hatch and the female molts and must develop again for another brood (Haahtela 1978).

Possible Misidentifications

The order Isopoda contains 10,000 species, 1/2 of which are marine and comprise 10 suborders, with eight present from central California to Oregon (see Brusca et al. 2007). Among isopods with elongated telsons (with anuses and uropods that are subterminal), there are several families including Flabellifera, Anthuridea, Gnathiidea, Epicaridea and Valvifera. The Valvifera are characterized by hinged doors or valves covering the pleopods, well-developed coxal plates, the absence of mandibular palps, occasionally fused pleonites and males with modified sexual appendages arising from the first pleonite, rather than the thorax. This suborder includes three local families and 34 species: the Chaetiliidae, the Arturidae and the Idoteidae (see *Idotea resecata* and *I. wosnesenskii*, this guide). The Arturidae is composed of species with narrow but cylindrical bodies, with the anterior four

pleopods larger and less setose than the posterior three. The Idoteidae is composed of 22 local species and characteristics of the group include a dorso-ventrally compressed body, similar pereopods, and seven free pereonites (Brusca et al. 2007). The Idoteidae includes those species with a pleon composed of two complete and one incomplete pleonite(s), a maxillipedal palp with five articles and one coupling seta, eyes that are not elongated transversely and a large shield-like pleotelson (Brusca et al. 2007).

Among the *Idotea*, *I. urotoma*, *I. rufescens*, and *I. ochotensis* have a maxillipedal palp with four articles (rather than five in the remaining eight *Idotea* species). Of the *Idotea* species with five maxillipedal palp articles, *I. aculeata*, a reddish idoteid, has a long projection on its narrowing pleotelson. It has oval eyes (not reniform), long antennae and blunt lateral borders on the first pleonite. *Idotea montereyensis* is slender and small (up to 16 mm), red, green-brown, or black and white and is found on or amongst *Phyllospadix* species and red algae. It has a rounded telson and with a short projection. *Idotea stenops* is olive-green to brown, found on brown algae and with narrow eyes, a slender pointed telson, and 2–3 coupling hooks on its maxillipeds, not one. *Idotea schmitti* has pleonite one with acute lateral borders and an anterior margin of pereonite one that does not encompass the cephalon. *Idotea kirchanskii* is bright green and found on *Phyllospadix* species. It has a rounded telson (lacking a medial projection), oval eyes and the epimera of pereonite somites are visible dorsally only on segments 5–7.

(The following characteristics are from descriptions of the genus as *Saduria*, and, thus, we use this name (see **Taxonomy**) (Rafi and Laubitz 1990)). *Saduria* (= *Mesidotea*) and *Idotea* species are similar in that their maxillipedal palps have 4–5 articles and their abdomens have 4–5 segments. *Saduria* species can be distinguished from other idoteid genera by their dorsal eyes, most idoteids have essentially dorsolateral eyes (see Fig. 1 *I. resecata*, Fig. 1 *I. wosnesenskii*). *Saduria* species are also very large and occur in brackish or fresh water, which is unusual in

the family. Furthermore, *Saduria* species have an abdomen with five segments, rather than four in *Idotea* and uropods are biramous, rather than uniramous in *Idotea*. Furthermore, *Saduria* species have a cephalon that is incised laterally, which is not the case in *Idotea* (Rafi and Laubitz 1990).

Mesidotea entomon is the only local species in the family Chaetiliidae, however, there are only two other northern Pacific species of *Saduria*. *Saduria sibirica* is a small (8.8 mm) Siberian species which occurs only as far east as Alaska. It is short and broad, not long and narrow and its thoracic epimera are blunt, not pointed. Its telson is short, not elongate (Schultz 1969). *Saduria sabini* is a blind species, up to 20 mm long. Unlike *M. entomon*, its head has posterior lobes which are produced and the second antennal flagellum has only six articles (Richardson 1905). *Saduria sabini* is a circumpolar species, found on beaches with muddy bottoms.

Synidotea species have maxilliped palps with 3 segments and an abdomen with 1–3 segments. In *Synidotea* species, there are no visible thoracic epimeral sutures. All abdominal pleonites are coalesced (showing only one lateral suture). The maxilliped palp has three articles and the flagellum (of the second antenna) has many joints (Miller 1975). *Chiridotea* species also have maxilliped palp with three articles as well as mandibles with no molar processes. This genus is similar to *Saduria*, but it occurs only in the Atlantic.

Ecological Information

Range: Type region is the northeast Atlantic. Known range is circumpolar from the west coast of North America south to Puget Sound, Washington (Kozloff 1974) and Pacific Grove, California (Richardson 1905). Also in freshwater European lakes (Hatch 1947) and has been introduced to the Black Sea (Kvach 2009). *Mesidotea entomon* is often called a “glacial relict” as populations in the Baltic are believed to have been isolated there by glacial advance and recession (Croghan and Lockwood 1968; Hagerman and Szaniawska 1991).

Local Distribution: Oregon distribution includes the Columbia River estuary,

particularly the lower reaches, and Florence (Hatch 1947).

Habitat: Highly variable from marine mud bottoms, small bays and inlets, on beaches buried in sand, and under rocks (Schultz 1969) to freshwater lakes (Hatch 1947). Least abundant in sand and gravel (McCrimmon and Bray 1962). *Mesidotea entomon* is a common species used in toxicity testing (e.g. petroleum, Percy 1978; hydrogen sulfide, Vismann 1991).

Salinity: An effective osmoregulator (Croghan and Lockwood 1968; Percy 1984; Carey 1991) that is mostly marine, but also found in brackish water, occasionally in fresh water (Kozloff 1974) and may prefer low salinity (Alaska, (MacGinitie 1955)). Although all other idoteids are marine, *M. entomon* has been found in deep Scandinavian (Brusca 1984) and Canadian (Korcznski 1991) freshwater lakes where individuals exhibit a very high tolerance to a range of salinities (e.g. 0 to more than 35 at 12°C or below, Hagerman and Szaniawska 1991) and commonly reside at salinities of 6–8. Furthermore, individuals have high tolerance to low oxygen and sulphide concentrations, with some populations reported to survive anoxia for up to 12 days (Hagerman and Szaniawska 1990; Modig and Olafsson 1998). In marine populations, males mature at larger sizes and females are larger and produce more eggs than freshwater populations (Narver 1968; Korcznski 1991).

Temperature: Very high tolerance to a range of temperatures (Percy 1984; Hagerman and Szaniawska 1991) from -1.3 to +10.0 C° reported (Beaufort Sea, McCrimmon and Bray 1962). Extreme cold temperatures may limit distribution (Schultz 1969).

Tidal Level: Highly variable. In the Arctic, individuals prefer shallow water (above 13 meters, MacGinitie 1955). However, *M. entomon* populations are also found on beaches and subtidally to as deep as to 813 meters (mid-California, Schultz 1969).

Associates:

Abundance: On Canadian Arctic muddy bottoms, abundances reached 0.46–0.93 individuals per gram per square meter (McCrimmon and Bray 1962). By far the most abundant isopod in Alaskan shallow waters with a sex-skewed ratio of seven females for every one male (MacGinitie 1955).

Life-History Information

Reproduction: Most isopods have separate sexes (i.e. dioecious, Brusca and Iverson 1985) (although protogynous and protandric species are known, Araujo et al. 2004; Boyko and Wolff 2014). Reproduction proceeds by copulation and internal fertilization where eggs are deposited within a few hours after copulation and brooded within the female marsupium (Brusca and Iverson 1985). The biphasic molting of isopods allows for copulation; the posterior portion of the body molts and individuals mate, then the anterior portion, which holds the brood pouch, molts (Sadro 2001). Embryonic development proceeds within the brood chamber and is direct before individuals hatch as manca larvae, resembling small adults, with no larval stage (Boyko and Wolff 2014).

Breeding in *M. entomon* can occur all year (Alaska, MacGinitie 1955) but probably occurs in summer months in the Arctic, where individuals die after reproducing once (McCrimmon and Bray 1962). Male penial styles form a tube for transmission of sperm and ova move into the brood pouch through genital ducts, which open onto the ventral surface of fifth abdominal pleonite. Oviducts are on each lateral edge, close to oostegite attachments, and end in fimbria within the body cavity. Juveniles hatch from May–June at lengths of approximately 3 mm (Bothnian Sea, Leonardsson 1986). The brood size is highly variable. Females were ovigerous from January to May and carried 153 eggs for several months before hatching in the Bothnian Sea (Leonardsson 1986). In an arctic marine population, the number of larvae carried by a single female ranged from 482–776 (MacGinitie 1955 in Narver 1968) while the average in Chignik Lake, Alaska was 92 larvae per brood (Narver 1968).

Larva: Since most isopods are direct developing, they lack a definite larval stage. Instead young developmental stages resemble small adults (e.g. Fig. 40.1, Boyko and Wolff 2014). Most isopods develop from embryo to a manca larva, consisting of three stages. Manca larvae are recognizable by lacking the seventh pair of pereopods, but otherwise resemble small adults. They usually hatch from the female marsupium at the second stage and the molt from second to third manca produces the seventh pair of

pereopods and sexual characteristics (Boyko and Wolff 2014). Isopod development and larval morphology can vary between groups (e.g. Gnathiidae, Cryptoniscoidea, Bopyroidae, Cymothoidae, Oniscoidea) (see Boyko and Wolff 2014). Parasitic isopods, for example, have larvae that are morphologically dissimilar from adults (Sadro 2001). Isopod larvae are not common members of the plankton, with parasitic larvae most likely to be observed. Occasionally, suspended benthic juveniles or pelagic species are collected in plankton samples, but these can be differentiated from larvae by their larger size (Sadro 2001). Recruitment is positively correlated to densities of the amphipod *Monoporeia affinis*, as cannibalism amongst *M. entomon* is higher in areas of low amphipod density (Sparrivek and Leonardsson 1998).

Juvenile: Juvenile development follows the third manca stage, where males have gonopods (modified first pleopods) and females have plate-like limbs on pereopods 2–5, called oostegites (that, together with the sternites, form the marsupium) (Boyko and Wolff 2014). Juvenile *M. entomon* have fewer second antennal flagellum articles than adults (Richardson 1905). Immature males have a ridged inner edge of pleopod two, where penial process will develop, as well as beginnings of penes on seventh thoracic somite (ventral). Immature females have oostegite "buds" inside bases of pereopods (ventral) (Schultz 1969). Individuals reach sexual maturity after 2–3 years (Bothnian Sea, Leonardsson 1986; Korcznski 1991), males usually before females with females reach maturing at 23–36 mm (Leonardsson 1986).

Longevity:

Growth Rate: Growth among isopods occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007), however, isopods do not autotomize limbs as readily as other groups (Brusca and Iverson 1985). Compared to other arthropods, isopods exhibit a unique biphasic molting, in which the posterior 1/2 of the body molts

before the anterior 1/2 (Haahtela 1978; Brusca et al. 2007).

Young of the year grow to less than 50 mm (McCrimmon and Bray 1962).

Food: An omnivore, predator and scavenger (Leonardsson 1986; Carey 1991), *M. entomon* is known to eat small crustaceans, from the plankton or benthos (e.g. euphausiids, McCrimmon and Bray 1962; copepods, Narver 1968; amphipods, Sparrivek and Leonardsson 1998), fish (e.g. sculpin, salmon, Narver 1968). Several individuals ate a 100–200 mm pygmy whitefish (*Prosopium coulteri*) within 10 hours (Chignik Lake, Alaska, Narver 1968).

Predators: Isopods play a significant role as intermediate food web links, like amphipods, (e.g. see *Americorophium salmonis*, this guide), that are consumed by more than 20 species of marine fish (McCrimmon and Bray 1962; Narver 1968; Welton and Miller 1980) and whales (Brusca et al. 2007). Cannibalism is also common in *M. entomon*, particularly between individuals of disparate sizes (Sparrivek and Leonardsson 1998).

Behavior:

Bibliography

1. ARAUJO, P. B., A. F. QUADROS, M. M. AUGUSTO, and G. BOND-BUCKUP. 2004. Postmarsupial development of *Atlantoscia floridana* (van Name, 1940) (Crustacea, Isopoda, Oniscidea): sexual differentiation and size at onset of sexual maturity. *Invertebrate Reproduction and Development*. 45:221-230.
2. BOYKO, C. B., and C. WOLFF. 2014. Isopoda and Tanaidacea, p. 210-215. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
3. BRUSCA, R. C. 1984. Phylogeny evolution and biogeography of the marine isopod subfamily Idoteinae (Crustacea: Isopoda: Idoteidae). *Transactions of the San Diego Society of Natural History*. 20:99-133.
4. BRUSCA, R. C., C. R. COELHO, and S. TAITI. 2007. Isopoda, p. 503-541. *In: The Light and Smith manual: intertidal invertebrates from central California to*
5. BRUSCA, R. C., and E. W. IVERSON. 1985. A guide to the marine isopod crustacea of Pacific Costa Rica. *Revista de Biología Tropical*. 33:1-77.
6. CAREY, A. G. 1991. Ecology of North American Arctic continental shelf benthos: a review. *Continental Shelf Research*. 11:865-883.
7. CROGHAN, P. C., and A. P. LOCKWOOD. 1968. Ionic regulation of Baltic and fresh-water races of Isopod *Mesidotea (Saduria) entomon* (L). *Journal of Experimental Biology*. 48:141-&.
8. HAAHTELA, I. 1978. Morphology as evidence of maturity in isopod Crustacea, as exemplified by *Mesidotea entomon* (L). *Annales Zoologici Fennici*. 15:186-190.
9. HAGERMAN, L., and A. SZANIAWSKA. 1990. Anaerobic metabolic strategy of the glacial relict isopod *Saduria (Mesidotea) entomon*. *Marine Ecology Progress Series*. 59:91-96.
10. —. 1991. Ion regulation under anoxia in the brackish water isopod *Saduria (Mesidotea) entomon*. *Ophelia*. 33:97-104.
11. HATCH, M. H. 1947. The Chelifera and isopoda of Washington and adjacent regions. University of Washington Publications in Biology. 10:155-274.
12. KORCZNSKI, R. E. 1991. Fecundity and age structure of freshwater and marine populations of the polar isopod *Mesidotea entomon* (L). *Invertebrate Reproduction and Development*. 20:45-48.
13. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
14. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to*

- Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
15. KVACH, Y. 2009. First report of *Saduria (Mesidotea) entomon* (Linnaeus, 1758) (Isopoda: Chaetiliidae) in the Black Sea. *Aquatic Invasions*. 4:393-395.
 16. LEONARDSSON, K. 1986. Growth and reproduction of *Mesidotea entomon* (Isopoda) in the northern Bothnian Sea. *Holarctic Ecology*. 9:240-244.
 17. MACGINITIE, G. E. 1955. Distribution and ecology of the marine invertebrates of Point Barrow, Alaska. Smithsonian Institution, Washington.
 18. MCCRIMMON, H., and J. BRAY. 1962. Observations on the Isopod *Mesidotea entomon* in the Western Canadian Arctic Ocean. *Journal of the Fisheries Research Board of Canada*. 19:489-496.
 19. MILLER, M. A. 1975. Phylum Arthropoda: Crustacea, Tanaidacea and Isopoda, p. 277-312. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
 20. MODIG, H., and E. OLAFSSON. 1998. Responses of Baltic benthic invertebrates to hypoxic events. *Journal of Experimental Marine Biology and Ecology*. 229:133-148.
 21. NARVER, D. W. 1968. Isopod *Mesidotea entomon* in Chignik Lakes, Alaska. *Journal of the Fisheries Research Board of Canada*. 25:157-167.
 22. NOMENCLATURE, I. C. O. Z. 1963. Opinion 643. *Idotea* Fabricius, 1798, and *Mesidotea* Richardson, 1905 (Crustacea, Decapoda); validation under the Plenary Powers. *Bulletin of Zoological Nomenclature*. 20:18-25.
 23. —. 1964. Addendum to opinion 643. *Bulletin of Zoological Nomenclature*. 21:92-93.
 24. PERCY, J. A. 1978. Effects of chronic exposure to petroleum upon growth and molting of juveniles of Arctic marine isopod crustacean *Mesidotea entomon*. *Journal of the Fisheries Research Board of Canada*. 35:650-656.
 25. —. 1985. Temperature tolerance, salinity tolerance, osmoregulation, and water permeability of Arctic marine isopods of the *Mesidotea (=Saduria)* complex. *Canadian Journal of Zoology*. 63:28-36.
 26. RAFI, F., and D. R. LAUBITZ. 1990. The Idoteidae (Crustacea, Isopoda, Valvifera) of the shallow waters of the northeastern north Pacific Ocean. *Canadian Journal of Zoology*. 68:2649-2687.
 27. RICHARDSON, H. 1905. Monograph on the isopods of North America. *Bulletin of the United States Natural Museum*. 54:1-727.
 28. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
 29. SADRO, S. 2001. Arthropoda: Decapoda, p. 176-178. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 30. SCHULTZ, G. A. 1969. How to know the marine isopod crustaceans. Brown Company, Dubuque, Iowa.
 31. SPARREVIK, E., and K. LEONARDSSON. 1998. Recruitment in the predacious isopod *Saduria entomon* (L.): alternative prey reduces cannibalism. *Journal of Experimental Marine Biology and Ecology*. 221:117-130.
 32. VISMANN, B. 1991. Physiology of sulfide detoxification in the isopod *Saduria (Mesidotea) entomon*. *Marine Ecology Progress Series*. 76:283-293.
 33. WELTON, L. L., and M. A. MILLER. 1980. Isopoda and Tanaidacea: the isopods and allies, p. 536-558. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.

Updated 2015

Detonella papillicornis

A sow bug

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Isopoda, Oniscidea
Family: Detonidae

Taxonomy: *Detonella papillicornis* was originally described by Richardson in 1904 as *Trichoniscus papillicornis*. Richardson described “about seven” articles on the flagellum of antenna two, but Lohmander later found 4–5 articles (including observations of the type specimen) and moved this species to a new genus, *Detonella* (Schultz 1972; Garthwaite 1988). Interspecific variation in characters (e.g. protopodite setae and pleotelson margin, Schmidt 2000) lead subsequent taxonomists to name new species, which were eventually synonymized as *D. papillicornis* (for full list of synonyms see Schmidt 2000).

Description

Size: Individuals 3.8 mm (Friday Harbor, Washington, Hatch 1947) to 6 mm in length (South Slough of Coos Bay).

Color: Body dark red and white mottled (Miller 1975).

General Morphology: Isopod bodies are dorso-ventrally flattened and can be divided into a compact **cephalon**, with eyes, two **antennae** and **mouthparts**, and a **pereon** (thorax) with eight segments, each bearing similar **pereopods** (hence the name “isopod”). Posterior to the pereon is the **pleon**, or abdomen, with six segments, the last of which is fused with the telson (the **pleotelson**) (see Plate 231, Brusca et al. 2007). The Isopoda can be divided into two groups: ancestral (“short-tailed”) groups (i.e. suborders) that have short telsons and derived (“long-tailed”) groups with long telsons, *D. papillicornis* groups among the former (see Fig. 9, Garthwaite and Lawson 1992; Brandt and Poore 2003; see Plate 249C, Brusca et al. 2007). The suborder, Oniscidea is the largest isopod suborder and the only fully-terrestrial crustacean group (Brusca et al. 2007).

Cephalon: Cephalon without rostrum, but slightly pronounced anteriorly and with concavity at apex (Fig. 2). Large anterior lobes at antero-lateral angles.

Rostrum: Absent (Fig. 2).

Eyes: Eyes with approximately eight (sometimes six) ocelli (Lohmander 1927).

Antenna 1: First antenna is vestigial among the suborder Oniscoidea.

Antenna 2: Peduncle of second antenna with 5–6 joints and the last three bear setose tubercles. The fifth joint has a distal process (Fig. 3) and the flagellum is composed of four articles (Richardson 1905; Schultz 1972).

Mouthparts:

Pereon: Body elongate and depressed with thorax composed of seven segments, the first of which is not fused with the head (Brusca et al. 2007).

Pereonites: Thoracic segments about equal in size, each with two rows of tubercles and postero-lateral angles directed backwards (Lohmander 1927).

Pereopods: Seven pairs of pereopods.

Pleon: Pleon narrower than pereon, but not abruptly so (Fig. 1).

Pleonites: Five free pleonites are present (Brusca et al. 2007) (Fig. 1).

Pleopods:

Uropods: Styliform and extend beyond body with outer branch stouter and longer than the inner branch. Uropods are inserted postero-laterally, and the base is not expanded (Fig. 4).

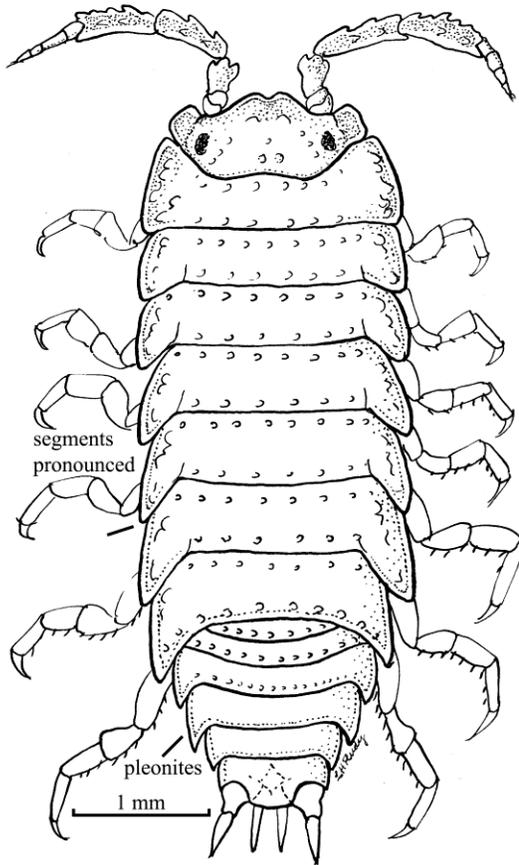
Pleotelson: Spatulate (Fig. 4) and morphologically variable. The pleotelson of the present specimen is more triangular in original description (Richardson 1905).

Sexual Dimorphism: The first and second pleopods are also elongated in males for copulation in oniscideans and reproductive females have a conspicuous marsupium.

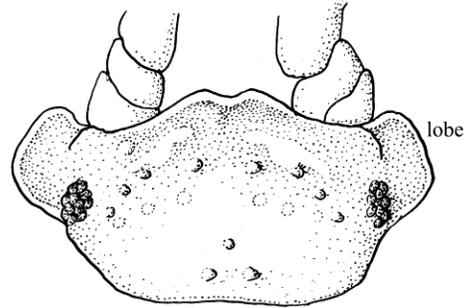
Possible Misidentifications

The order Isopoda contains 10,000 species, 1/2 of which are marine and comprise 10 suborders, with eight present from central California to Oregon (see Brusca et al. 2007). Among isopods with small, short telsons, there are several groups (i.e. suborders) including Phreatoicidea, Asellota,

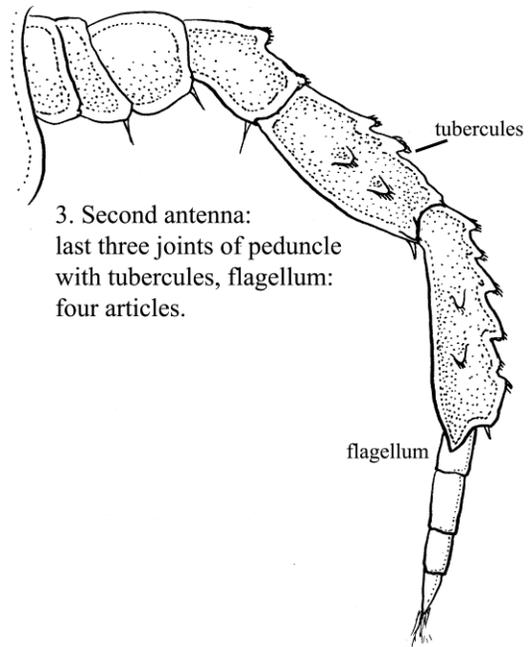
Detonella papillicornis



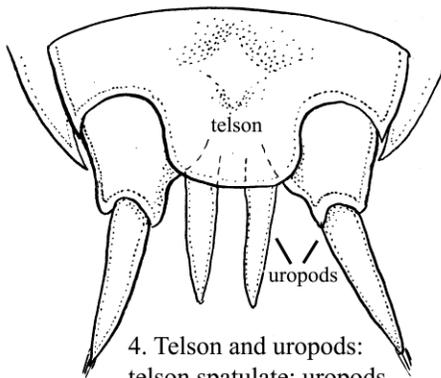
1. *Detonella papillicornis* (L: 6mm) x25:
thoracic segments extend backwards;
abdomen with five free pleonites.



2. Head:
no rostrum, simple eyes;
large lateral lobes.



3. Second antenna:
last three joints of peduncle
with tubercles, flagellum:
four articles.



4. Telson and uropods:
telson spatulate; uropods
styliform; bases not
expanded.

Microcerberidea, Calabozoidea and Oniscidea.

The monophyletic Oniscidea (previously part of the paraphyletic Scyphacidae, see Holdrich et al. 1984 in Schmidt 2000, 2002) is a fully-terrestrial group composed of 4,000 described species, with 22 known locally (among 10 families, Schmidt 2002; Brusca et al. 2007). Members are characterized by seven pereonites, the first not fused with the head, seven pairs of pereopods, male penes on the sternum of pereonite seven, a pleotelson that does not curve dorsally, vestigial (or very small) antennules and a pleon with five free pleonites (Brusca et al. 2007). The first and second pleopods are also elongated in males for copulation, many species have a water conducting system and some have respiratory structures on pleopods called pseudotracheae.

The Detonidae have antennae flagella with four articles and the family comprises four species locally, three of which are in the genus *Armadilloniscus*; *Detonella* is monotypic locally (*D. papillicornis* is the only species). *Armadilloniscus* species have a definite rostrum and an oval body with no narrowing of the pleon. Their uropods have expanded bases and all four branches (which are small) are near the center line. The exopods are inserted on the medial margin in *Armadilloniscus* and are terminal in *Detonella* and conspicuously extend from body outline (Brusca et al. 2007). *Armadilloniscus lindahli* has a convex body and can roll into a ball. *Armadilloniscus coronacapitalis* has a spur-like extension on the lateral margin of the antenna peduncle article while *A. holmesi* does not. Both *A. lindahli* and *A. coronacapitalis* have a southern distribution from Marin County, California south, while *D. papillicornis* occurs from San Francisco Bay, California northward (Brusca et al. 2007). *Armadilloniscus holmesi* occurs from Friday Harbor, Washington to Bahia Magdalena, Baja California (Schultz 1972).

Ecological Information

Range: Type region is Alaska (*Trichoniscus papillicornis*, USNM# 28772, Garthwaite and Lawson 1992). Essentially an Arctic and Antarctic species (Lohmander 1927) with known range from Southern Alaska, to

Washington and, recently, in San Francisco Bay area (Garthwaite and Lawson 1992).

Local Distribution: Coos Bay distribution at Day's Creek in the South Slough.

Habitat: Preferable substrates include sand and beach debris.

Salinity:

Temperature:

Tidal Level: Upper intertidal of beaches.

Associates: The amphipod, *Orchestra* and other Oniscoidea, including *Armadilloniscus tuberculatus* and *Philoscia richardsona* (Hatch 1947).

Abundance: Somewhat sparse locally, but rather common in littoral sites throughout San Francisco Bay, California (Garthwaite and Lawson 1992).

Life-History Information

Reproduction: Most isopods have separate sexes (i.e. dioecious, Brusca and Iverson 1985) (although protogynous and protandric species are known, Araujo et al. 2004; Boyko and Wolff 2014). Reproduction proceeds by copulation and internal fertilization where eggs are deposited within a few hours after copulation and brooded within the female marsupium (Brusca and Iverson 1985). The biphasic molting of isopods allows for copulation; the posterior portion of the body molts and individuals mate, then the anterior portion, which holds the brood pouch, molts (Sadro 2001). Embryonic development proceeds within the brood chamber and is direct with individuals hatching as manca larvae that resemble small adults, with no larval stage (Boyko and Wolff 2014).

Larva: Since most isopods are direct developing, they lack a definite larval stage. Instead this young developmental stage resembles small adults (e.g. Fig. 40.1, Boyko and Wolff 2014). Most isopods develop from embryo to a manca larva, consisting of three stages. Manca larvae are recognizable by lacking the seventh pair of pereopods, but otherwise resemble small adults. They usually hatch from the female marsupium at the second stage and the molt from second to third manca produces the seventh pair of pereopods and sexual characteristics (Boyko and Wolff 2014). Isopod development and larval morphology can vary between groups (e.g. Gnathiidae, Cryptoniscoidea, Bopyroidae, Cymothoidae) (see Boyko and Wolff 2014) and some oniscid isopod species are known to care for their young after

hatching (Boyko and Wolff 2014). Parasitic isopods, for example, have larvae that are morphologically dissimilar from adults (Sadro 2001). Isopod larvae are not common members of the plankton, with parasitic larvae most likely to be observed. Occasionally, suspended benthic juveniles or pelagic species are collected in plankton samples, but these can be differentiated from larvae by their larger size (Sadro 2001).

Juvenile:

Longevity:

Growth Rate: Growth among isopods occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autonomized (Kuris et al. 2007), however, isopods do not autotomize limbs as readily as other groups (Brusca and Iverson 1985). Compared to other arthropods, isopods exhibit a unique biphasic molting, in which the posterior 1/2 of the body molts before the anterior 1/2 (Brusca et al. 2007).

Food:

Predators: Isopods play a significant role as intermediate food web links, like amphipods, (e.g. see *Americorophium salmonis*, this guide) that are consumed by more than 20 species of marine fish (Welton and Miller 1980; cabezon, Best and Stachowicz 2012) and whales (Brusca et al. 2007).

Behavior:

Bibliography

1. ARAUJO, P. B., A. F. QUADROS, M. M. AUGUSTO, and G. BOND-BUCKUP. 2004. Postmarsupial development of *Atlantoscia floridana* (van Name, 1940) (Crustacea, Isopoda, Oniscidea): sexual differentiation and size at onset of sexual maturity. *Invertebrate Reproduction and Development*. 45:221-230.
2. BEST, R. J., and J. J. STACHOWICZ. 2012. Trophic cascades in seagrass meadows depend on mesograzers: variation in feeding rates, predation susceptibility, and abundance. *Marine Ecology Progress Series*. 456:29-42.
3. BOYKO, C. B., and C. WOLFF. 2014. Isopoda and Tanaidacea, p. 210-215. *In: Atlas of Crustacean Larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
4. BRANDT, A., and G. C. B. POORE. 2003. Higher classification of the flabelliferan and related isopoda based on a reappraisal of relationships. *Invertebrate Systematics*. 17:893-923.
5. BRUSCA, R. C., C. R. COELHO, and S. TAITI. 2007. Isopoda, p. 503-541. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
6. BRUSCA, R. C., and E. W. IVERSON. 1985. A guide to the marine isopod crustacea of Pacific Costa Rica. *Revista de Biología Tropical*. 33:1-77.
7. GARTHWAITE, R. L. 1988. *Detonella papillicornis* (Richardson) (Isopoda: Oniscidea: Scyphacidae) from Bolinas Lagoon, California. *Bulletin Southern California Academy of Sciences*. 87:46-47.
8. GARTHWAITE, R. L., and R. LAWSON. 1992. Oniscidea isopoda of the San Francisco Bay area. *Proceedings of the California Academy of Sciences*. 47:303-328.
9. HATCH, M. H. 1947. The Chelifera and isopoda of Washington and adjacent regions. *University of Washington Publications in Biology*. 10:155-274.
10. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
11. LOHMANDER, H. 1927. On some terrestrial isopods in the United States. *Proceedings of the United States Natural Museum*. 72:1-18.
12. MILLER, M. A. 1975. Phylum Arthropoda: Crustacea, Tanaidacea and Isopoda, p. 277-312. *In: Light and Smith manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
13. RICHARDSON, H. 1905. Monograph on the isopods of North America.

- Bulletin of the United States Natural Museum. 54:727.
14. SADRO, S. 2001. Arthropoda: Decapoda, p. 176-178. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 15. SCHMIDT, C. 2000. Revision of *Detonella* Lohmander, 1927 (Crustacea, Isopoda, Oniscoidea). *Mitteilungen aus dem Museum fuer Naturkunde in Berlin Zoologische Reihe*. 76:51-60.
 16. —. 2002. Contribution to the phylogenetic system of the Crinocheta (Crustacea, Isopoda). Part 1. (Olibrinidae to Scyphacidae s. str.). *Mitteilungen aus dem Museum fuer Naturkunde in Berlin Zoologische Reihe*. 78:275-352.
 17. SCHULTZ, G. A. 1972. A review of species of the family Scyphacidae in the New World (Crustacea, Isopoda, Oniscoidea). *Proceedings of the Biological Society of Washington*. 84:477-487.
 18. WELTON, L. L., and M. A. MILLER. 1980. Isopoda and Tanaidacea: The Isopods

Updated 2015

Idotea resecata

A valviferan isopod

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Isopoda
Family: Idoteidae

Taxonomy: The genus *Idotea* was described by Fabricius in 1798, and although originally spelled *Idotea*, several authors adopted the spelling *Idothea*, since then. The genus *Pentidotea* was described by Richardson in 1905 and was reduced to subgeneric level by Menzies in 1950. The two subgenera (or genera), *Pentidotea* and *Idotea* differ by the articles on maxilliped palps, the former with five and the latter with four (Miller and Lee 1970), but are not always currently recognized (Rafi and Laubitz 1990). Furthermore, this character may vary with age and other characters may reveal more concrete differences to define the two (Poore and Ton 1993). Thus synonyms for *I. resecata* include, *Idothea resecata*, *Pentidotea resecata* and *Idotea Pentidotea resecata*. *Idothea rufescens* may also be a synonym having been described from an immature specimen (Menzies and Waidzunus 1948). We follow the most recent intertidal guide for the northeast Pacific coast (Brusca et al. 2007), which uses the name *Idotea resecata*.

Description

Size: Individuals 39–50 mm in length (Ricketts and Calvin 1952; Welton and Miller 1980) and can be 4 ½ times longer than wide (Richardson 1905).

Color: Light green, with black chromatophores when closely associated with *Zostera* and yellowish-brown when on kelp (Ricketts and Calvin 1952; Welton and Miller 1980). The body color is a result of carotenoids and carotenoproteins (for carotenoid pigments, see Lee and Gilchrist 1972) within the cuticle and may serve as camouflage from fish predation (Best and Stachowicz 2012). Color polymorphism is high in the congener, *I. baltica* and variation is determined by habitat and predation pressure but not sexual selection (Jormalainen and Merilaita 1995).

General Morphology: Isopod bodies are dorso-ventrally flattened and can be divided into a compact **cephalon**, with eyes, two **antennae** and **mouthparts**, and a **pereon**

(thorax) with eight segments, each bearing similar **pereopods** (hence the name “isopod”). Posterior to the pereon is the **pleon**, or abdomen, with six segments, the last of which is fused with the telson (the **pleotelson**) (see Plate 231, Brusca et al. 2007). The Isopoda can be divided into two groups: ancestral (“short-tailed”) groups (i.e. suborders) that have short telsons and derived (“long-tailed”) groups with long telsons. Valviferan (including the Idoteidae) are a distinct group of isopods (Brusca 1984) and have an elongated telson (Fig. 73, Ricketts and Calvin 1952).

Cephalon: Entire, not notched (compare to *Mesidotea entomon*, this guide), sides of head straight. First thoracic segment fused with head (Isopoda, Brusca et al. 2007).

Rostrum: Slight rostrum (Fig. 3) with frontal process narrow, pointed and exceeding frontal lamina visible from ventral side (Fig. 2).

Eyes: Eyes oval, not markedly elongate transversely (Fig. 3).

Antenna 1:

Antenna 2: The number of flagellum segments on the second antennae increase with individual size (Menzies and Waidzunus 1948).

Mouthparts: Maxilliped palp with five articles (although juveniles may have only four, Poore and Ton 1993) and one coupling hook (Fig. 4). The number of setae on the maxilliped increases with individual size (Menzies and Waidzunus 1948).

Pereon: Body elongate and depressed with thorax composed of seven segments (Fig. 1) (Brusca et al. 2007).

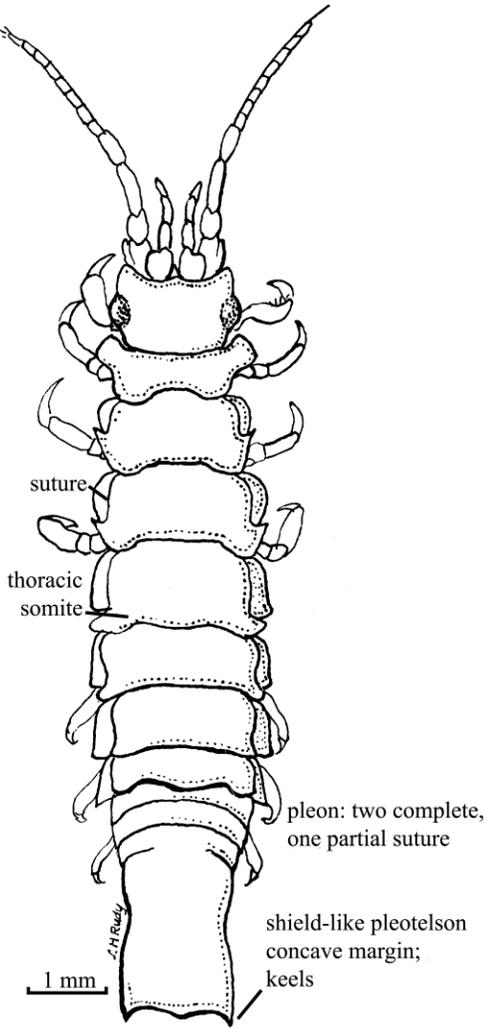
Pereonites: All seven thoracic somites (pereonites) are free (Idoteidae) with epimeral sutures visible dorsally (except the first somite) (Fig. 1).

Pereopods: Seven pairs of ambulatory and similar walking legs (Fig. 1).

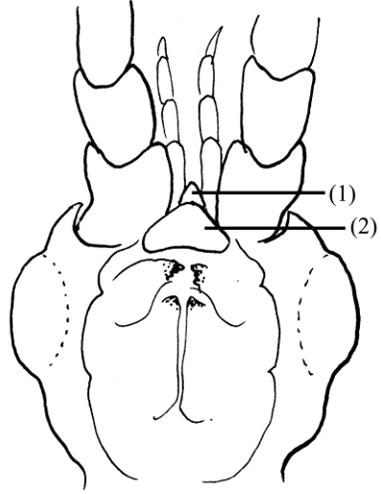
Pleon: Short pleon with six pleonites (Brusca et al. 2007).

Pleonites: Two pleonites complete, with one partial horizontal suture (Fig. 1).

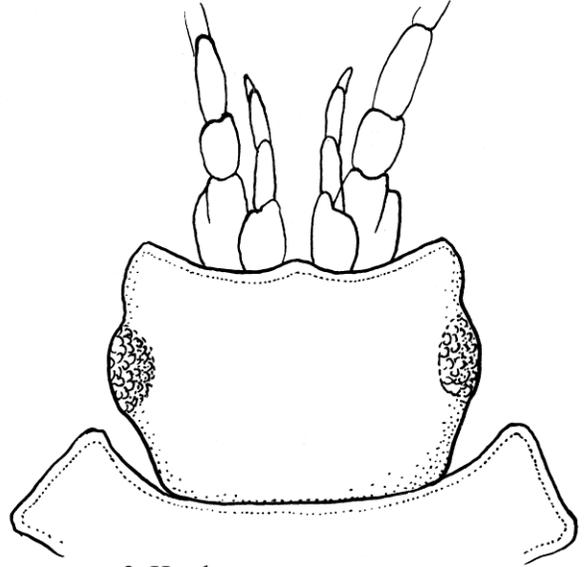
Idotea resecata



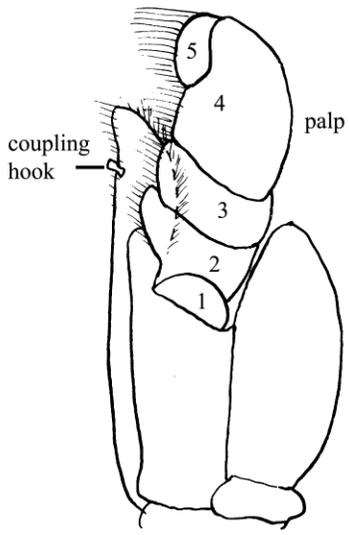
1. *Idotea resecata* x12:
 Idoteidae: body elongate, depressed, legs nearly alike, ambulatory; seven free thoracic segments.



2. Head (ventral view) x36:
 Frontal process (1) narrow, pointed, and exceeds frontal lamina (2).



3. Head:
 entire, not notched
 eyes not elongate or pear-shaped but oval; sides of head straight.



4. Maxilliped:
 one coupling hook
 five article palp.

Pleopods: Appendages of the pleon include five respiratory pairs and a single pair of uropods (Brusca et al. 2007). The first three pairs are particularly locomotory (e.g. for swimming), while the posterior two pairs are strictly respiratory (Alexander 1988; Alexander et al. 1995).

Uropods: Ventral, not visible dorsally, and forming opercular doors or valves covering pleopods (Valvifera).

Pleotelson: Large, elongated and shield-like with posterior border bearing concave margin, keels (Fig. 1).

Sexual Dimorphism: Conspicuous sexual dimorphism is rare among isopods. Mature females bear a thoracic marsupium and males have modified first pleopods, called gonopods (Sadro 2001; Boyko and Wolff 2014).

Possible Misidentifications

The order Isopoda contains 10,000 species, 1/2 of which are marine and comprise 10 suborders, with eight present from central California to Oregon (see Brusca et al. 2007). Among isopods with elongated telsons (with anuses and uropods that are subterminal), there are several families including Flabellifera, Anthuridea, Gnathiidea, Epicaridea and Valvifera. The Valvifera are characterized by hinged doors or valves covering the pleopods, well-developed coxal plates, the absence of mandibular palps, occasionally fused pleonites and males with modified sexual appendages arising from the first pleonite, rather than the thorax. This suborder includes three local families and 34 species: the Chaetiliidae (see *Mesidotia entomon*, this guide), the Arturidae and the Idoteidae. The Arturidae is composed of species with narrow but cylindrical bodies, with the anterior four pleopods larger and less setose than the posterior three. Characteristics of the Idoteidae include a dorso-ventrally compressed body, similar pereopods, and seven free pereonites and is composed of 22 species, locally (Brusca et al. 2007).

Most local species in the Idoteidae are within the genus *Idotea* (12 species), which includes those with a pleon composed of two complete and one incomplete pleonite(s), a maxillipedal palp with five articles and one coupling seta, eyes that are not elongated transversely and a large shield-like pleotelson (Brusca et al. 2007).

Idotea sensu Poore and Ton 1993 refers only to individuals with free pleonites, anterior spiniform pereopod setae and free penes, while many northeastern Pacific species have fused pleonites, partially fused penes and reduced coxae (Poore and Ton 1993). Based on these characters, authors differentiate *Idotea* from *Pentidotia* (see **Taxonomy**). *Idotea resecata* is the only member of the genus to have a concave pleotelson. Thus it is easy to distinguish it from other light green idoteids, such as *I. aculeata* and *I. montereyensis*.

Among the *Idotea*, *I. urotoma*, *I. rufescens*, and *I. ochotensis* have a maxillipedal palp with four articles (rather than five in the remaining eight *Idotea* species) a character that previously defined two subgenera, *Idotea Idotea* (with four articles) and *Idotea Pentidotia* (with five articles) (Menzies 1950; Miller and Lee 1970).

Of the *Idotea* species with five maxillipedal palp articles (*Idotea Pentidotia*, Menzies 1950), *I. aculeata*, a reddish idoteid, has a long projection on its narrowing pleotelson. It has oval eyes (not reniform), long antennae and blunt lateral borders on the first pleonite. *Idotea montereyensis* is slender and small (up to 16 mm), red, green-brown, or black and white and is found on *Phyllospadix* species and red algae. It has a rounded telson and with a short projection. *Idotea stenops* is olive-green to brown, found on brown algae and with narrow eyes, a slender pointed telson, and 2–3 coupling hooks on its maxillipeds, not one. *Idotea schmitti* has pleonite one with acute lateral borders and an anterior margin of pereonite one that does not encompass the cephalon. *Idotea kirchanskii* is bright green and found on *Phyllospadix* species. It has a rounded telson (lacking a medial projection), oval eyes and the epimera of pereonite somites are visible dorsally only on segments 5–7.

Ecological Information

Range: Type locality is Strait of Juan de Fuca (Menzies 1950). Known range is from Alaska to Baja, California (Ricketts and Calvin 1952; Iverson 1974; Welton and Miller 1980). *Idotea* as a genus is cosmopolitan (see Fig. 9, Brusca 1984).

Local Distribution: Coos Bay distribution northwest of the Charleston Bridge in South Slough.

Habitat: Frequently found on or clinging to eelgrass *Zostera* or *Macrocystis* (Ricketts and Calvin 1952; Miller 1975), even on drifting kelp rafts (Hobday 2000). Preferable substrate is mud, but individuals also occur under rocks, in crevices and cracks, within empty shells and worm tubes (Brusca et al. 2007).

Salinity: Can survive one hour in fresh water (Welton and Miller 1980).

Temperature: Scarce where surface temperatures exceed 18°C (Welton and Miller 1980). North Pacific *Idotea* species exhibit a wide temperature tolerance as their ranges extend across several zoogeographic provinces that are associated with temperature barriers for other invertebrates (Wallerstein and Brusca 1982).

Tidal Level: Intertidal, near + 0.15 meters (South Slough of Coos Bay), ranging from surface to 6.4 meters (Richardson 1905).

Associates: Gastropods and hermit crabs in the genera *Littorina* and *Pagurus*, as well as amphipods.

Abundance: Common in Puget Sound.

Life-History Information

Reproduction: Most isopods have separate sexes (i.e. dioecious, Brusca and Iverson 1985) (although protogynous and protandric species are known, Araujo et al. 2004; Boyko and Wolff 2014). Reproduction proceeds by copulation and internal fertilization where eggs are deposited within a few hours after copulation and brooded within the female marsupium (e.g. *I. emarginata*, Naylor 1955; Brusca and Iverson 1985). The biphasic molting of isopods allows for copulation; the posterior portion of the body molts and individuals mate, then the anterior portion, which holds the brood pouch, molts (Sadro 2001). Embryonic development proceeds within the brood chamber is direct and individuals hatch as manca larvae that resemble small adults, with no larval stage (see *I. granulosa* and *I. neglecta* development, Stromberg 1965; Boyko and Wolff 2014). Ovigerous *I. resicata* have been observed in July (central California, Welton and Miller 1980). *Idotea baltica* and *I. chelipes* produce 1–3 broods per year with brood sizes that range from 60 to 120 eggs per brood (Limfjord, Denmark, Kroer 1989; Baltic, Jormalainen and Tuomi 1989).

Larva: Since most isopods are direct developing, they lack a definite larval stage.

Instead this young developmental stage resembles small adults (e.g. Fig. 40.1, Boyko and Wolff 2014). Most isopods develop from embryo to a manca larva, consisting of three stages. Manca larvae are recognizable by lacking the seventh pair of pereopods, but otherwise resemble small adults. They usually hatch from the female marsupium at the second stage and the molt from second to third manca produces the seventh pair of pereopods and sexual characteristics (Boyko and Wolff 2014). Isopod development and larval morphology can vary between groups (e.g. Gnathiidae, Cryptoniscoidea, Bopyroidae, Cymothoidae, Oniscoidea) (see Boyko and Wolff 2014). Parasitic isopods, for example, have larvae that are morphologically dissimilar from adults (Sadro 2001). Isopod larvae are not common members of the plankton, with parasitic larvae most likely to be observed. Occasionally, suspended benthic juveniles or pelagic species are collected in plankton samples, but these can be differentiated from larvae by their larger size (Sadro 2001). The development of the congener *I. emarginata* was described in 1955 by Naylor where, within the brood chamber, three stages were observed over a 30 day period (at 9°C): 1) green eggs 700 µm in diameter encased in a membrane, 2) elongated embryo with rudimentary appendages and 3) hatched individuals, 1.8 mm in length, with fully formed appendages. Following hatching individuals molt every two weeks (British Isles, Naylor 1955).

Juvenile: Juvenile development follows the third manca stage, where males have gonopods (modified first pleopods) and females have plate-like limbs on pereopods 2–5, called oostegites (that, together with the sternites, form the marsupium) (Boyko and Wolff 2014). Females begin to brood once body length is at least 14 mm (Wallerstein and Brusca 1982).

Longevity: The longevity of the congeners, *Idotea baltica* and *I. chelipes* is 11–12 months and 10–11 months, respectively (Limfjord, Denmark, Kroer 1989).

Growth Rate: Growth among isopods occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007), however, isopods do not autotomize limbs as

readily as other groups (Brusca and Iverson 1985). Compared to other arthropods, isopods exhibit a unique biphasic molting, in which the posterior 1/2 of the body molts before the anterior 1/2 (Brusca et al. 2007).

Food: *Idotea ressecata* is an herbivore, primarily eating kelp, eelgrass blades (Welton and Miller 1980), sea grasses (Holbrook et al. 2000; Best and Stachowicz 2012) and their epiphytes (Williams and Ruckelshaus 1993; Houghes et al. 2010). Populations have the ability to destroy entire kelp canopies when predators are lacking (Bernstein and Jung 1979). *Idotea* species produce a phenolic compound that reduces feeding on eelgrass (*Zostera* species) by other grazers (e.g. *Ampithoe valida*, this guide) (Lewis and Boyer 2014). Algal feeding rates in *Idotea* species can range from 0.1–71.3 mg per individual per day (Trowbridge 1993).

Predators: Isopods play a significant role as intermediate food web links, like amphipods (e.g. see *Americorophium salmonis*, this guide), that are consumed by more than 20 species of marine fish (e.g. *Oxyjulis californica*, Bernstein and Jung 1979; Welton and Miller 1980; cabezon, Best and Stachowicz 2012) and whales (Brusca et al. 2007).

Behavior: Always orients on kelp blades, along the same axis as the blade. Swimming is accomplished by propulsion from the first three pairs of pleopods. In *Idotea ressecata* and *I. wosnesenskii*, the power strokes from each pleopod occur in succession, but the recovery strokes occur simultaneously (Alexander 1988).

Bibliography

1. ALEXANDER, D. E. 1988. Kinematics of swimming in two species of *Idotea* (Isopoda, Valvifera). *Journal of Experimental Biology*. 138:37-49.
2. ALEXANDER, D. E., J. BLODIG, and S. Y. HSIEH. 1995. Relationship between function and mechanical properties of the pleopods of isopod crustaceans. *Invertebrate Biology*. 114:169-179.
3. ARAUJO, P. B., A. F. QUADROS, M. M. AUGUSTO, and G. BOND-BUCKUP. 2004. Postmarsupial development of *Atlantoscia floridana* (van Name, 1940) (Crustacea, Isopoda, Oniscidea): sexual differentiation and size at onset of sexual maturity. *Invertebrate Reproduction and Development*. 45:221-230.
4. BERNSTEIN, B. B., and N. JUNG. 1979. Selective pressures and coevolution in a kelp canopy community in southern California. *Ecological Monographs*. 49:335-355.
5. BEST, R. J., and J. J. STACHOWICZ. 2012. Trophic cascades in seagrass meadows depend on mesograzers: variation in feeding rates, predation susceptibility, and abundance. *Marine Ecology Progress Series*. 456:29-42.
6. BOYKO, C. B., and C. WOLFF. 2014. Isopoda and Tanaidacea, p. 210-215. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
7. BRUSCA, R. C. 1984. Phylogeny evolution and biogeography of the marine isopod subfamily Idoteinae (Crustacea: Isopoda: Idoteidae). *Transactions of the San Diego Society of Natural History*. 20:99-133.
8. BRUSCA, R. C., C. R. COELHO, and S. TAITI. 2007. Isopoda, p. 503-541. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
9. BRUSCA, R. C., and E. W. IVERSON. 1985. A guide to the marine isopod crustacea of Pacific Costa Rica. *Revista de Biologia Tropical*. 33:1-77.
10. HOBDAV, A. J. 2000. Persistence and transport of fauna on drifting kelp (*Macrocystis pyrifera* (L.) C. Agardh) rafts in the Southern California Bight. *Journal of Experimental Marine Biology and Ecology*. 253:75-96.
11. HOLBROOK, S. J., D. C. REED, K. HANSEN, and C. A. BLANCHETTE. 2000. Spatial and temporal patterns of predation on seeds of the surfgrass *Phyllospadix torreyi*. *Marine Biology*. 136:739-747.
12. HUGHES, A. R., R. J. BEST, and J. J. STACHOWICZ. 2010. Genotypic diversity and grazer identity interactively influence seagrass and

- grazer biomass. Marine Ecology Progress Series. 403:43-51.
13. IVERSON, E. W. 1974. Range extensions for some California marine isopod crustaceans. Bulletin Southern California Academy of Sciences. 73:164-169.
 14. JORMALAINEN, V., S. MERILAITA, and J. TUOMI. 1995. Differential predation on sexes affects color polymorphism of the isopod *Idotea baltica* (Pallas). Biological Journal of the Linnean Society. 55:45-68.
 15. JORMALAINEN, V., and J. TUOMI. 1989. Reproductive ecology of the isopod *Idotea baltica* (Pallas) in the northern Baltic. Ophelia. 30:213-223.
 16. KROER, N. 1989. Life cycle characteristics and reproductive patterns of *Idotea spp.* (Isopoda) in the Limfjord, Denmark. Ophelia. 30:63-74.
 17. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 18. LEE, W. L., and B. M. GILCHRIST. 1972. Pigmentation color change and the ecology of the marine isopod *Idotea resicata* (Stimpson) 1857. Journal of Experimental Marine Biology and Ecology. 10:1-27.
 19. LEWIS, J. T., and K. E. BOYER. 2014. Grazer functional roles, induced defenses, and indirect interactions: implications for eelgrass restoration in San Francisco Bay. Diversity. 6:751-770.
 20. MENZIES, R. J. 1950. The taxonomy, ecology, and distribution of northern California isopods of the genus *Idothea* with the description of a new species. Wasmann Journal of Biology. 8:155-195.
 21. MENZIES, R. J., and R. J. WAIDZUNAS. 1948. Postembryonic growth changes in the isopod *Pentidotea resicata* (Stimpson), with remarks on their taxonomic significance. Biological Bulletin. 95:107-113.
 22. MILLER, M. A. 1975. Phylum Arthropoda: Crustacea, Tanaidacea and Isopoda, p. 277-312. *In*: Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
 23. MILLER, M. A., and W. L. LEE. 1970. A new idoteid isopod *Idotea (Pentidotea) kirchanskii* from central California (Crustacea). Proceedings of the Biological Society of Washington. 82:790-798.
 24. NAYLOR, E. 1955. The life cycle of the isopod *Idotea emarginata* (Fabricius). Journal of Animal Ecology. 24:270-281.
 25. POORE, G. C. B., and H. M. L. TON. 1993. Idoteidae of Australia and New Zealand (Crustacea: Isopoda: Valvifera). Invertebrate Taxonomy. 7:197-278.
 26. RAFI, F., and D. R. LAUBITZ. 1990. The Idoteidae (Crustacea, Isopoda, Valvifera) of the shallow waters of the northeastern north Pacific Ocean. Canadian Journal of Zoology. 68:2649-2687.
 27. RICHARDSON, H. 1905. Monograph on the isopods of North America. Bulletin of the United States Natural Museum. 54:727.
 28. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
 29. SADRO, S. 2001. Arthropoda: Decapoda, p. 176-178. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 30. STROMBERG, J. O. 1965. On the embryology of the isopod *Idotea*. Arkiv for Zoologi. 17:421-473.
 31. TROWBRIDGE, C. D. 1993. Feeding ecology of the ascoglossan opisthobranch *Aplysiopsis enteromorphae* (Cockerell and Eliot): patterns of distribution and impact on tidepool-dwelling green algae. Journal of Experimental Marine Biology and Ecology. 169:233-257.

32. WALLERSTEIN, B. R., and R. C. BRUSCA. 1982. Fish predation: a preliminary study of its role in the zoogeography and evolution of shallow water idoteid isopods (Crustacea: Isopoda: Idoteidae). *Journal of Biogeography*. 9:135-150.
33. WELTON, L. L., and M. A. MILLER. 1980. Isopoda and Tanaidacea: the isopods and allies, p. 536-558. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
34. WILLIAMS, S. L., and M. H. RUCKELSHAUS. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. *Ecology*. 74:904-918.

Updated 2015

Idotea wosnesenskii

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Isopoda
Family: Idoteidae

Taxonomy: The genus *Idotea* was described by Fabricius in 1798, and although originally spelled *Idotea*, several authors adopted the spelling *Idothea*, since then. The genus *Pentidotea* was described by Richardson in 1905 and was reduced to subgeneric level by Menzies in 1950. The two subgenera (or genera), *Pentidotea* and *Idotea* differ by the articles on maxilliped palps, the former with five and the latter with four (Miller and Lee 1970), but are not always currently recognized (Rafi and Laubitz 1990). Furthermore, this character may vary with age and other characters may reveal more concrete differences to define the two (Poore and Ton 1993). Thus synonyms for *I. wosnesenskii* include, *Idothea wosnesenskii*, *Pentidotea wosnesenskii* and *Idotea Pentidotea wosnesenskii*. We follow the most recent intertidal guide for the northeast Pacific coast (Brusca et al. 2007), which uses the name *Idotea wosnesenskii*.

Description

Size: Individuals to 35 mm in length (Hatch 1947) and $\frac{1}{2}$ to $\frac{1}{3}$ as wide as long (Fee 1927; Ricketts and Calvin 1952). The figured specimen (male) is 22 mm long. A 22-mm male weighs approximately 0.3 grams and a similar sized female weighs 0.2 grams (wet weight).

Color: Dark green or light olive and some individuals living amongst red algae are dark red and gray (Fee 1927). Males tend to be larger and paler than females (Welton and Miller 1980). Color polymorphism is high in the congener, *I. baltica* and variation is determined by habitat and predation pressure but not sexual selection (Jormalainen and Merilaita 1995).

General Morphology: Isopod bodies are dorso-ventrally flattened and can be divided into a compact **cephalon**, with eyes, two **antennae** and **mouthparts**, and a **pereon** (thorax) with eight segments, each bearing similar **pereopods** (hence the name “isopod”). Posterior to the pereon is the **pleon**, or abdomen, with six segments, the last of which is fused with the telson (the **pleotelson**) (see

Plate 231, Brusca et al. 2007). The Isopoda can be divided into two groups: ancestral (“short-tailed”) groups (i.e. suborders) that have short telsons and derived (“long-tailed”) groups with long telsons. Valviferan (including the Idoteidae) isopods have an elongated telson (Fig. 73, Ricketts and Calvin 1952). *Idotea wosnesenskii* individuals are robust, not tapered, elongate and depressed (see Fig. 62, Ricketts and Calvin 1952).

Cephalon: Wider than long, with frontal margin slightly concave (Miller 1968) and posterior portion somewhat wider than anterior portion (Richardson 1905). Head narrower than pleon (Schultz 1969). First thoracic segment fused with head (Isopoda, Brusca et al. 2007).

Rostrum: Frontal process widely angulate and hidden by and not extending beyond frontal lamina, which is triangulate (in dorsal view) (Fig. 2).

Eyes: Eyes small, reniform (kidney-shaped) (Miller 1975) (Fig. 4), compound, transversely ovate and situated at extreme lateral margins (compare to *M. entomon*, this guide), about halfway between the anterior and posterior margins (Fig. 1).

Antenna 1: First antennae (antennules) with four articles, basal one large and flattened.

Antenna 2: Second antennae with peduncle of five articles and flagellum of 12–16 articles (Fig. 1).

Mouthparts: Maxilliped palp with five articles and one coupling hook (Miller 1975).

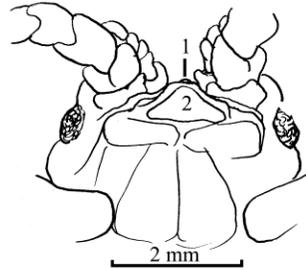
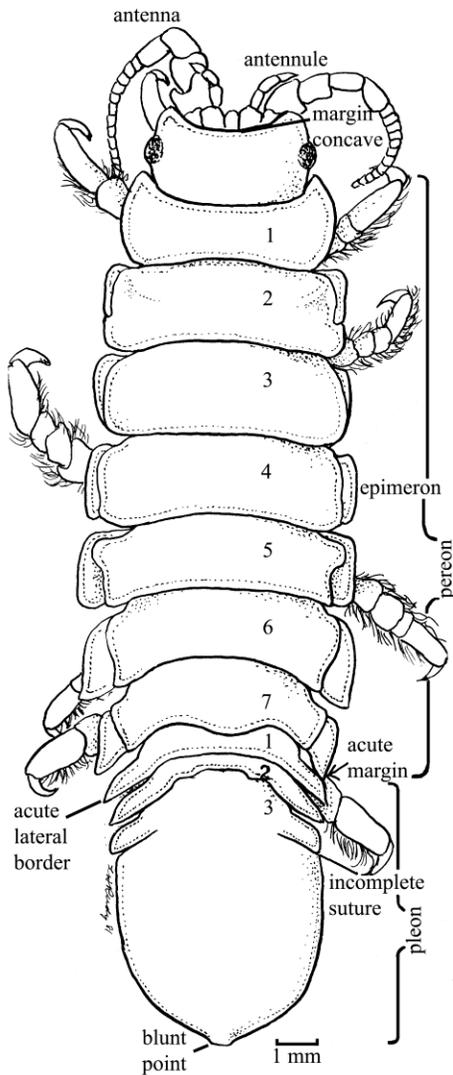
Pereon: Body elongate and depressed with thorax composed of seven segments (Brusca et al. 2007).

Pereonites: All seven thoracic somites (pereonites) are free (Idoteidae) with epimeral sutures visible dorsally (except the first somite) (Fig. 1). Postero-lateral border of last pereonite acute (Fig. 1).

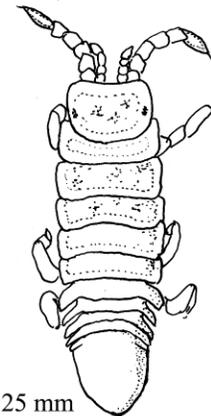
Pereopods: Seven pairs of ambulatory and similar walking legs.

Pleon: Short pleon with six pleonites (Brusca et al. 2007). Pleon with two complete and one partial intersegmental suture dividing it

Idotea wosnesenskii

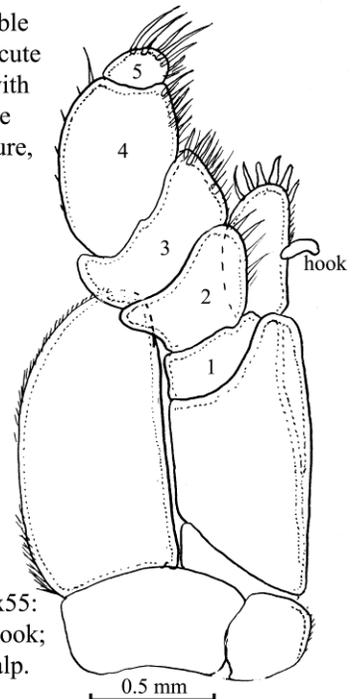


2. Head (ventral view) x12:
frontal process (1) hidden by
frontal lamina (2).

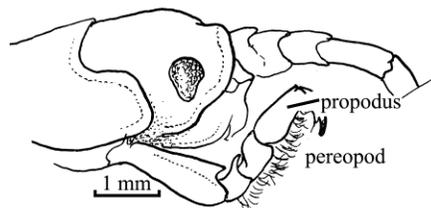


3. Young x7.5:
actual length 8.25 mm
short antennal flagella. 1 mm

1. *Idotea wosnesenskii* (L: 22mm W:6.6mm) ♀ x7.5:
body elongate, not tapered; dark green; head
narrower than pleon, frontal margin concave;
eyes at lateral margins
seven free pereonites, six visible
epimera; last pereonite with acute
posterolateral border. Pleon with
2 pointed pleonites, shield-like
pleotelson, an incomplete suture,
and a blunt terminal point.



5. Maxilliped x55:
one coupling hook;
five-articled palp.



4. Head (lateral view) x12:
eyes reniform; pereopods hairy.

into three divisions. Pleon wider than head (Schultz 1969).

Pleonites: Two small anterior pleonites and a large shield-like pleotelson with an incompletely fused pleonite near its base (Fig. 1) (Miller 1975). The first pleonite with acute lateral borders and shorter laterally than medially (Miller 1975; Kozloff 1974) (Fig 1).

Pleopods: Seven pleopod pairs are ambulatory, nearly similar and all with small sharp claws. Male pereopods with coarse hairs (Figs. 1, 4) and females with hair only on propodi. Appendages of the pleon include five respiratory pairs and a single pair of uropods (Brusca et al. 2007). The first three pairs are particularly locomotory (e.g. for swimming), while the posterior two pairs are strictly respiratory (Alexander 1988; Alexander et al. 1995), although all five pairs can also function in ventilation as water is passed through the branchial chamber with a total of three strokes (Alexander 1991).

Uropods: Ventral, not visible dorsally, and forming opercular plates or valves.

Pleotelson: Large, shield-like, broadly rounded (Hatch 1947), and ends in large blunt point (Fig. 1).

Sexual Dimorphism: Conspicuous sexual dimorphism is rare among isopods, however, males tend to be larger, paler, and have hairier legs than females in *I. wosnesenskii*. Mature females are broader and bear a thoracic marsupium while males have modified first pleopods, called gonopods (Sadro 2001; Boyko and Wolff 2014).

Possible Misidentifications

The order Isopoda contains 10,000 species, 1/2 of which are marine and comprise 10 suborders, with eight present from central California to Oregon (see Brusca et al. 2007). Among isopods with elongated telsons (with anuses and uropods that are subterminal), there are several families including Flabellifera, Anthuridea, Gnathiidea, Epicaridea and Valvifera. The Valvifera are characterized by hinged doors or valves covering the pleopods, well-developed coxal plates, the absence of mandibular palps, occasionally fused pleonites and males with modified sexual appendages arising from the first pleonite, rather than the thorax. This suborder includes three local families and 34 species: the Chaetiliidae (see *Mesidotea entomon*,

this guide), the Arturidae and the Idoteidae. The Arturidae is composed of species with narrow but cylindrical bodies, with the anterior four pleopods larger and less setose than the posterior three. Characteristics of the Idoteidae include a dorso-ventrally compressed body, similar pereopods, and seven free pereonites and is composed of 22 species, locally (Brusca et al. 2007).

Most local species in the Idoteidae are within the genus *Idotea* (12 species), which includes those with a pleon composed of two complete and one incomplete pleonite(s), a maxillipedal palp with five articles and one coupling seta, eyes that are not elongated transversely and a large shield-like pleotelson (Brusca et al. 2007). *Idotea sensu* Poore and Ton 1993 refers only to individuals with free pleonites, anterior spiniform pereopod setae and free penes, while many northeastern Pacific species have fused pleonites, partially fused penes and reduced coxae (Poore and Ton 1993). Based on these characters, authors differentiate *Idotea* from *Pentidotea* (see **Taxonomy**).

Among the *Idotea*, *I. urotoma*, *I. rufescens*, and *I. ochotensis* have a maxillipedal palp with four articles (rather than five in the remaining eight *Idotea* species) a character that previously defined two subgenera, *Idotea Idotea* (with four articles) and *Idotea Pentidotea* (with five articles) (Menzies 1950; Miller and Lee 1970).

Of the *Idotea* species with five maxillipedal palp articles (*Idotea Pentidotea*, Menzies 1950), *I. aculeata*, a reddish idoteid with a long projection on its narrowing pleotelson. It has oval eyes (not reniform), long antennae and blunt lateral borders on the first pleonite (compare to acute borders as in *I. wosnesenskii*). *Idotea montereyensis* is slender and small (up to 16 mm), red, green-brown, or black and white and is found on *Phyllospadix* species and red algae. It has a rounded telson and with a short projection. It differs from *I. wosnesenskii* in the frontal process, which is narrow, pointed and projects much beyond the frontal lamina. The frontal lamina is triangulate (compare to *I. wosnesenskii*, frontal process and Fig. 2). Male *I. montereyensis* are long and slim and females are broader, and more like *I. wosnesenskii* in outline. *Idotea schmitti* has pleonite one with acute lateral borders as in *I. wosnesenskii*, but the anterior margin of pereonite one does not encompass the

cephalon. *Idotea stenops* is olive-green to brown, found on brown algae and with narrow eyes, a slender pointed telson, and 2–3 coupling hooks on its maxillipeds, not one. *Idotea kirchanskii* is bright green and found on *Phyllospadix* species. It has a rounded telson (lacking a medial projection), oval eyes and the epimera of pereonal somites are visible dorsally only on segments 5–7. *Idotea resecata* (this guide) has a very distinctive concave pleotelson that is not a rounded, but convex.

Ecological Information

Range: No exact type locality is given, but region (based on noted locations in the original species description) is likely Sea of Okhotsk and Bering Sea (Menzies 1950). Known range from Sea of Okhotsk, Russia, Bering Sea, Alaska (Menzies 1950), south to San Luis Obispo, Calif. (Ricketts and Calvin 1952; Kussakin 1994).

Local Distribution: Oregon distribution in Coos (e.g. at Pigeon Point) and Tillamook Bays (Hatch 1947).

Habitat: Substrates include rocks and pilings (Puget Sound, Washington Kozloff 1974), but individuals also occur under rocks on gravelly or sandy substrates with lots of vegetative debris as well as in crevices and cracks, within empty shells and worm tubes (Brusca et al. 2007). Also in mussel beds, on *Ulva* and *Porphyra* (Welton and Miller 1980). More common on outer rocky shores than in estuaries (Menzies 1950; Ricketts and Calvin 1952).

Salinity: Tolerates salinity changes better than *I. resecata* (Brusca 1966; Welton and Miller 1980). Primary osmoregulation (i.e. inward ion transport) occurs with the endopodites of the posterior three pleopods (Holliday 1988).

Temperature: North Pacific *Idotea* species exhibit a wide temperature tolerance as their ranges extend across several zoogeographic provinces that are associated with temperature barriers for other invertebrates (Wallerstein and Brusca 1982).

Tidal Level: Upper middle intertidal zone to 16 m deep. The figured specimen was collected at 0.0 meters.

Associates: Associates include the gastropod *Tegula*, brachyurans *Hemigrapsus* species and *Cancer oregonensis*, and the carnivorous gastropod, *Nucella*. Often co-

occurs with mussel species in large clusters (Ricketts and Calvin 1952).

Abundance: Common and probably the most common idoteid isopod in Coos Bay (Kozloff 1974; Menzies 1950). Most common small crustacean in Santa Cruz, California (Ricketts and Calvin 1952).

Life-History Information

Reproduction: Most isopods have separate sexes (i.e. dioecious, Brusca and Iverson 1985) (although protogynous and protandric species are known, Araujo et al. 2004; Boyko and Wolff 2014). Reproduction proceeds by copulation and internal fertilization where eggs are deposited within a few hours after copulation and brooded within the female marsupium (Brusca and Iverson 1985). The biphasic molting of isopods allows for copulation; the posterior portion of the body molts and individuals mate, then the anterior portion, which holds the brood pouch, molts (Sadro 2001). Embryonic development proceeds within the brood chamber and is direct with individuals hatching as manca larvae that resemble small adults, with no larval stage (Boyko and Wolff 2014). Little is known about reproduction and development in *I. wosnesenskii* specifically, but females are ovigerous in July (California, Welton and Miller 1980) and a few advanced (8 mm) juveniles were found in female oöestigites in April (Coos Bay). *Idotea baltica* and *I. chelipes* produce 1–3 broods per year with brood sizes that range from 60 to 120 eggs per brood (Limfjord, Denmark, Kroer 1989; Baltic, Jormalainen and Tuomi 1989).

Larva: Since most isopods are direct developing, they lack a definite larval stage. Instead this young developmental stage resembles small adults (e.g. Fig. 40.1, Boyko and Wolff 2014). Most isopods develop from embryo to a manca larva, consisting of three stages. Manca larvae are recognizable by lacking the seventh pair of pereopods, but otherwise resemble small adults. They usually hatch from the female marsupium at the second stage and the molt from second to third manca produces the seventh pair of pereopods and sexual characteristics (Boyko and Wolff 2014). Isopod development and larval morphology can vary between groups (e.g. Gnathiidae, Cryptoniscoidea, Bopyroidae, Cymothoidae, Oniscoidea) (see Boyko and Wolff 2014). Parasitic isopods, for example, have larvae that are morphologically

dissimilar from adults (Sadro 2001). Isopod larvae are not common members of the plankton, with parasitic larvae most likely to be observed. Occasionally, suspended benthic juveniles or pelagic species are collected in plankton samples, but these can be differentiated from larvae by their larger size (Sadro 2001).

Juvenile: Juveniles possess most adult characteristics, but antennal flagellae are shorter than in adults (Fig. 3). This specimen was found in a female brood pouch. Juvenile development in isopods follows the third manca stage, where males have gonopods (modified first pleopods) and females have plate-like limbs on pereopods 2–5, called oostegites (that, together with the sternites, form the marsupium) (Boyko and Wolff 2014). Females brood beginning when body length is 13 mm (Wallerstein and Brusca 1982).

Longevity:

Growth Rate: Growth among isopods occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007), however, isopods do not autotomize limbs as readily as other groups (Brusca and Iverson 1985). Compared to other arthropods, isopods exhibit a unique biphasic molting, in which the posterior 1/2 of the body molts before the anterior 1/2 (Brusca et al. 2007).

Food: *Idotea wosnesenskii* is primarily an herbivore, eating kelp and eelgrass blades (Welton and Miller 1980). However, *I. wosnesenskii* individuals are also known to chew through and ingest egg capsules of the gastropod, *Nucella emarginata* (Rawlings 1990). *Idotea* species produce a phenolic compounds that reduces feeding on eelgrass (*Zostera* species) by other grazers (e.g. *Ampithoe valida*, this guide) (Lewis and Boyer 2014). Regarding the intertidal alga, *Iridaea cordata*, *Idotea wosnesenskii* only fed on reproductively mature plants (Gaines 1985). A feeding rate of approximately 3 mg per day of the unicellular epiphytes, *Isthmia nervosa* and *Odonthalia floccosa* (Ruesink 2000) was reported and overall, algal feeding rates in *Idotea* species can range from 0.1–71.3 mg per individual per day (Trowbridge 1993). *Idotea wosnesenskii* is not negatively affected by macroalgal defenses (e.g. acrylic acid)

(VanAlstyne et al. 2001) unlike many grazers (e.g. *Strongylocentrotus* species).

Predators: Isopods play a significant role as intermediate food web links, like amphipods, (e.g. see *Americorophium salmonis*, this guide) that are consumed by more than 20 species of marine fish (Welton and Miller 1980; cabezon, Best and Stachowicz 2012) and whales (Brusca et al. 2007).

Behavior: Swimming is accomplished by propulsion from the first three pairs of pleopods. In *Idotea ressecata* and *I. wosnesenskii*, the power strokes from each pleopod occur in succession, but the recovery strokes occur simultaneously (Alexander 1988).

Bibliography

1. ALEXANDER, D. E. 1988. Kinematics of swimming in two species of *Idotea* (Isopoda, Valvifera). *Journal of Experimental Biology*. 138:37-49.
2. —. 1991. Mechanics of branchial ventilation in the valviferan isopod *Idotea wosnesenskii* (Crustacea). *Journal of Zoology*. 224:607-616.
3. ALEXANDER, D. E., J. BLODIG, and S. Y. HSIEH. 1995. Relationship between function and mechanical properties of the pleopods of isopod crustaceans. *Invertebrate Biology*. 114:169-179.
4. ARAUJO, P. B., A. F. QUADROS, M. M. AUGUSTO, and G. BOND-BUCKUP. 2004. Postmarsupial development of *Atlantoscia floridana* (van Name, 1940) (Crustacea, Isopoda, Oniscidea): sexual differentiation and size at onset of sexual maturity. *Invertebrate Reproduction and Development*. 45:221-230.
5. BEST, R. J., and J. J. STACHOWICZ. 2012. Trophic cascades in seagrass meadows depend on mesograzers: variation in feeding rates, predation susceptibility, and abundance. *Marine Ecology Progress Series*. 456:29-42.
6. BOYKO, C. B., and C. WOLFF. 2014. Isopoda and Tanaidacea, p. 210-215. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.

7. BRUSCA, G. J. 1966. Studies on the salinity and humidity tolerances of five species of isopods in a transition from marine to terrestrial life. *Bulletin of the Southern California Academy of Science*. 65:147-154.
8. BRUSCA, R. C., C. R. COELHO, and S. TAITI. 2007. Isopoda, p. 503-541. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
9. BRUSCA, R. C., and E. W. IVERSON. 1985. A guide to the marine isopod crustacea of Pacific Costa Rica. *Revista de Biología Tropical*. 33:1-77.
10. FEE, A. R. 1927. The Isopoda of Departure Bay and vicinity with descriptions of new species, variations and colour notes. *Contributions to Canadian Biology and Fisheries*. 3:15-47.
11. GAINES, S. D. 1985. Herbivory and between-habitat diversity: the differential effectiveness of defenses in a marine plant. *Ecology*. 66:473-485.
12. HATCH, M. H. 1947. The Chelifera and isopoda of Washington and adjacent regions. *University of Washington Publications in Biology*. 10:155-274.
13. HOLLIDAY, C. W. 1988. Branchial Na⁺/K⁺-atpase and osmoregulation in the isopod, *Idotea wosnesenskii*. *Journal of Experimental Biology*. 136:259-272.
14. JORMALAINEN, V., S. MERILAITA, and J. TUOMI. 1995. Differential predation on sexes affects color polymorphism of the isopod *Idotea baltica* (Pallas). *Biological Journal of the Linnean Society*. 55:45-68.
15. JORMALAINEN, V., and J. TUOMI. 1989. Reproductive ecology of the isopod *Idotea baltica* (Pallas) in the northern Baltic. *Ophelia*. 30:213-223.
16. KOZLOFF, E. N. 1974. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago and adjacent Regions. University of Washington Press, Seattle and London.
17. KROER, N. 1989. Life cycle characteristics and reproductive patterns of *Idotea spp.* (Isopoda) in the Limfjord, Denmark. *Ophelia*. 30:63-74.
18. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
19. KUSSAKIN, O. G. 1994. The common north-east idoteid *Idotea wosnesenskii*, a recent invader to the Commander Islands. *Biologiya Morya*. 20:97-99.
20. LEWIS, J. T., and K. E. BOYER. 2014. Grazer functional roles, induced defenses, and indirect interactions: implications for eelgrass restoration in San Francisco Bay. *Diversity*. 6:751-770.
21. MENZIES, R. J. 1950. The taxonomy, ecology, and distribution of northern California isopods of the genus *Idothea* with the description of a new species. *Wasmann Journal of Biology*. 8:155-195.
22. MILLER, M. A. 1968. Isopoda and Tanaidacea from buoys in coastal waters of the continental United States, Hawaii, and the Bahamas (Crustacea). *Proceedings of the United States National Museum*. 125:1-53.
23. —. 1975. Phylum Arthropoda: Crustacea, Tanaidacea and Isopoda, p. 277-312. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
24. MILLER, M. A., and W. L. LEE. 1970. A new idoteid isopod *Idotea (Pentidotea) kirchanskii* from central California (Crustacea). *Proceedings of the Biological Society of Washington*. 82:790-798.
25. POORE, G. C. B., and H. M. L. TON. 1993. Idoteidae of Australia and New Zealand (Crustacea: Isopoda: Valvifera). *Invertebrate Taxonomy*. 7:197-278.
26. RAFI, F., and D. R. LAUBITZ. 1990. The Idoteidae (Crustacea, Isopoda, Valvifera) of the shallow waters of the northeastern north Pacific Ocean.

- Canadian Journal of Zoology. 68:2649-2687.
27. RAWLINGS, T. A. 1990. Associations between egg capsule morphology and predation among populations of the marine gastropod, *Nucella emarginata*. Biological Bulletin. 179:312-325.
 28. RICHARDSON, H. 1905. Monograph on the isopods of North America. Bulletin of the United States Natural Museum. 54:1-727.
 29. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides: an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford: Stanford University Press, Stanford.
 30. RUESINK, J. L. 2000. Intertidal mesograzers in field microcosms: linking laboratory feeding rates to community dynamics. Journal of Experimental Marine Biology and Ecology. 248:163-176.
 31. SADRO, S. 2001. Arthropoda: Decapoda, p. 176-178. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 32. SCHULTZ, G. A. 1969. How to know the marine isopod crustaceans. Brown Company, Dubuque, Iowa.
 33. TROWBRIDGE, C. D. 1993. Feeding ecology of the ascoglossan opisthobranch *Aplysiopsis enteromorphae* (Cockerell and Eliot): patterns of distribution and impact on tidepool-dwelling green algae. Journal of Experimental Marine Biology and Ecology. 169:233-257.
 34. VAN ALSTYNE, K. L., G. V. WOLFE, T. L. FREIDENBURG, A. NEILL, and C. HICKEN. 2001. Activated defense systems in marine macroalgae: evidence for an ecological role for DMSP cleavage. Marine Ecology Progress Series. 213:53-65.
 35. WALLERSTEIN, B. R., and R. C. BRUSCA. 1982. Fish predation: a preliminary study of its role in the zoogeography and evolution of shallow water idoteid isopods (Crustacea: Isopoda: Idoteidae). Journal of Biogeography. 9:135-150.
 36. WELTON, L. L., and M. A. MILLER. 1980. Isopoda and Tanaidacea: the isopods and allies, p. 536-558. *In*: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.

Updated 2015

Ianiropsis derjugini

An asellid isopod

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Isopoda, Asellota
Family: Janiridae

Taxonomy: In 1952, Menzies characterized *I. kincaidi* and *I. derjugini* as subspecies of *I. kincaidi* based on morphology and habitat. However, due to a lack of evidence of genetic introgression, most researchers consider them different species (e.g. Wilson and Wagele 1994; Brusca et al. 2007).

Description

Size: Up to 4 mm in length (Menzies 1952). Figured specimen (from Charleston, Coos Bay) was 3 mm long.

Color: White with brown chromatophores.

General Morphology: Isopod bodies are dorso-ventrally flattened and can be divided into a compact **cephalon**, with eyes, two **antennae** and **mouthparts**, and a **pereon** (thorax) with eight segments, each bearing similar **pereopods** (hence the name “isopod”). Posterior to the pereon is the **pleon**, or abdomen, with six segments, the last of which is fused with the telson (the **pleotelson**) (see Plate 231, Brusca et al. 2007). The Isopoda can be divided into two groups: ancestral (“short-tailed”) groups (i.e. suborders) that have short telsons and derived (“long-tailed”) groups with long telsons, *I. derjugini* groups among the former (see Plate 233C, Brusca et al. 2007). The suborder, Asellota is considered one of the ancestral isopod groups (see Fig. 7, Brandt and Poore 2003) and members are some of the most diverse isopods and are most successful in deep sea habitats (Brusca et al. 2007; e.g. *Jaera*, Linse et al. 2014).

Cephalon: Without rostrum or anteriorly projecting anterolateral angles (Fig. 1) (compare to *I. k. kincaidi*, Miller 1975).

Rostrum: Absent.

Eyes: Well-developed and reniform (Fig. 1).

Antenna 1: The first antenna is quite short and has a flagellum with 8–10 articles (Fig. 2) (10 articles in males, Richardson 1905).

Antenna 2: The second antenna is with “squama”, or scales, on third article of the base (Fig. 3) (Miller 1975) and is about $\frac{2}{3}$ length of body. The flagellum is with many

segments and fine setae and the peduncle has six articles (Hatch 1947).

Mouthparts: Maxilliped palps with articles two and three much wider than endite (not figured) (Miller 1975).

Pereon:

Pereonites: Seven thoracic segments with variably shaped epimera (Fig. 1) and no lateral spines.

Pereopods: The interior edge of the propodus is smooth, not serrated, on proximal third of the first pereopod (Fig. 4) (Miller 1975).

Pleon:

Pleonites:

Pleopods:

Uropods: Biramous with inner branch a little longer than the outer branch. The total uropod length is less than $\frac{1}{2}$ the pleotelson (Miller 1975) (Fig. 5).

Pleotelson: Shield-like with spineless lateral borders spineless (Fig. 1) and at postero-lateral angles at insertion of uropods (Fig. 1) (Miller 1975) (no other *Ianiropsis* has this character). Three posterior segments not differentiated (Hatch 1947).

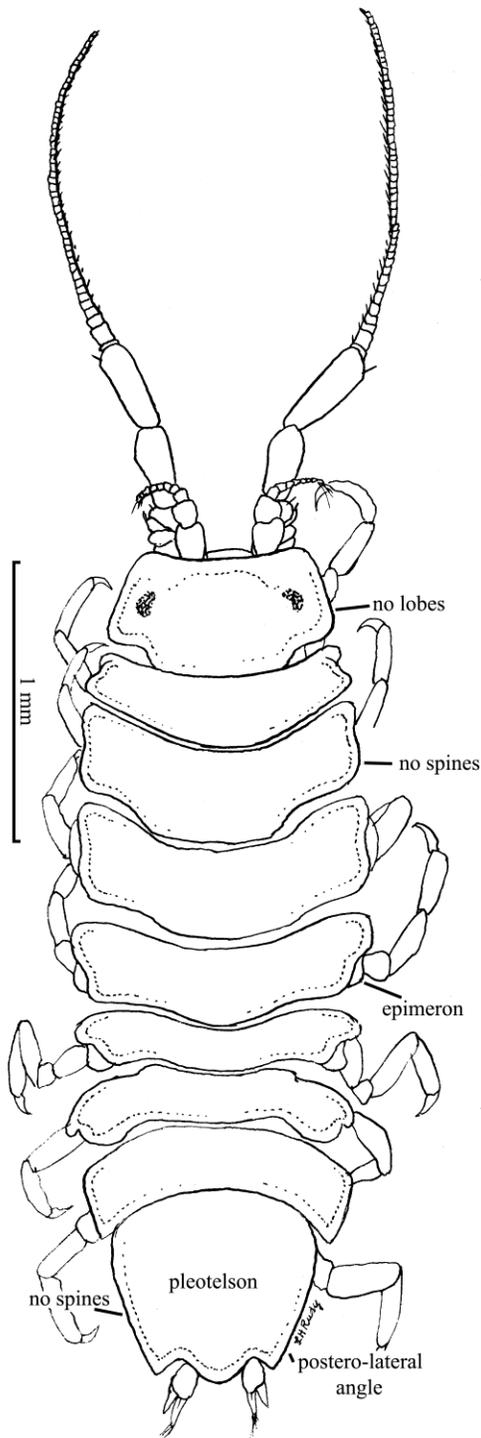
Sexual Dimorphism: Males have a second pleopod with modified copulatory morphology (enlarged protopod and knee-like endopod) (Brusca et al. 2007).

Possible Misidentifications

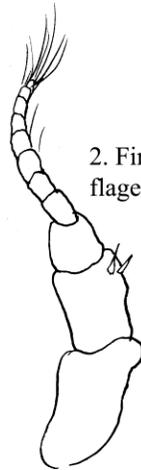
The order Isopoda contains 10,000 species, 1/2 of which are marine and comprise 10 suborders, with eight present from central California to Oregon (see Brusca et al. 2007). Among isopods with elongated telsons (with anuses and uropods that are subterminal), there are several groups (i.e. suborders) including Flabellifera, Anthuridea, Gnathiidea, Epicaridea and Valvifera.

The suborder Asellota is characterized by uropods that are styliform (Brandt and Poore 2003) and terminal, pleonites 3, 4 or 5 fused with the pleotelson, and 1–3 forming an operculum over those posterior and pereonites without coxal plates. Thirty-eight species comprising nine

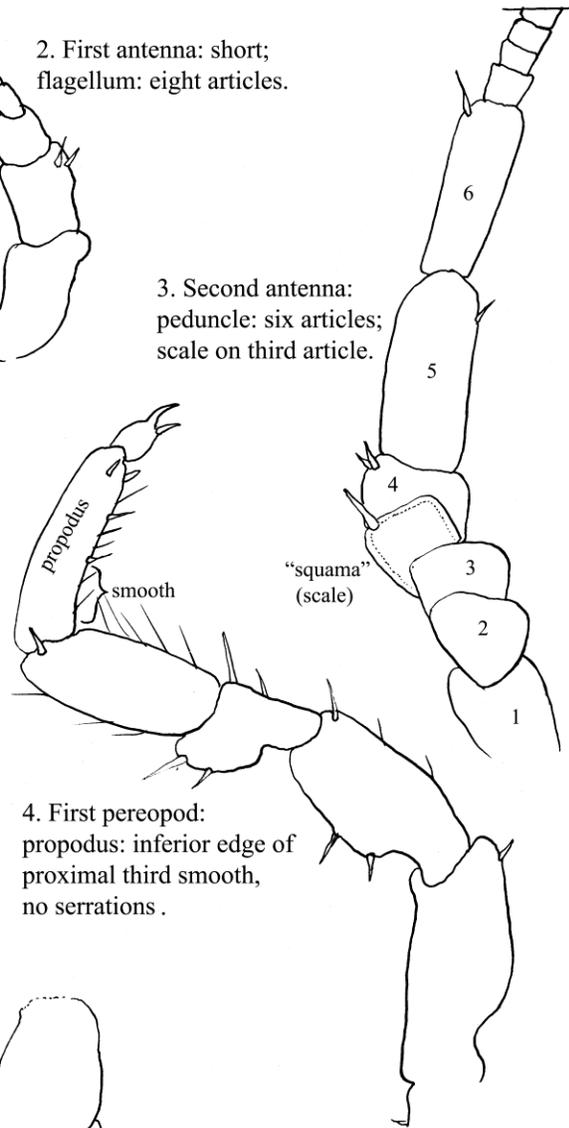
Ianiropsis derjugini



1. *Ianiropsis derjugini* (L: 3mm) x50:
head without lobes or rostrum;
thoracic epimera, pleotelson without spines;
second antenna 2/3 body length.



2. First antenna: short;
flagellum: eight articles.



3. Second antenna:
peduncle: six articles;
scale on third article.

4. First pereopod:
propodus: inferior edge of
proximal third smooth,
no serrations .



5. Right uropod:
two branches: inner longer;
length: less than pleotelson.

families are reported from central California to Oregon, but only 18 species are intertidal (Brusca et al. 2007).

The family Janiridae (174 species, 23 genera worldwide, Linse et al. 2014) is a non-monophyletic isopod family (Wilson 1994) that have 2–3 claws on the dactyls of pereopods 2–7, antennae with long flagella, and well developed uropods. There are 13 species locally and seven are in the genus *Ianiropsis*, all of which are found in the intertidal or shallow subtidal (Brusca et al. 2007). The remaining genera include *Caecianiropsis*, *Caecijaera*, *Iais* (each with one local species) and *Janiralata* (three local species).

Both *Ianiropsis kincaidi* and *I. derjugini* were formerly subspecies of *I. kincaidi* and thus, are most morphologically similar. *Ianiropsis kincaidi* has longer uropods, almost half to as long as pleotelson. Its first antennae are elongate and it lacks the postero-lateral angles of *I. derjugini*. Habitats of the two subspecies are different: *I. kincaidi* lives in small pools created by wave splash and is subject to wide temperature variation (Menzies 1952). On the other hand, *I. derjugini* is more common under rocks that are covered by algae (Brusca et al. 2007).

Ianiropsis analoga, *I. epilittoralis* and *I. tridens* have spine-like serrations on the sides of the pleotelson (Miller 1975). *Ianiropsis analoga* occurs from Marin County, California northward, *I. epilittoralis* can be found from Marin County south to San Luis Obispo, California in the high intertidal and *I. tridens* has a large range from San Juan Island, Washington to Monterey County, California as well as northern Chile. *Ianiropsis minuta* and *I. montereyensis* lack these serrations, however *I. minuta* can be recognized by evenly rounded head margins and the lack of the postero-lateral angles of the telson and *I. montereyensis* has uropods that are longer than the telson. The former species is reported from Marin County, California while the latter occurs from Marin to Monterey Counties in the intertidal and shallow subtidal zones (Brusca et al. 2007).

Ecological Information

Range: Type region is the Bering Sea. Known range from Komandorskie Islands,

Bering Sea to Monterey County, California (Miller 1968).

Local Distribution: Coos Bay distribution at the Charleston small boat basin.

Habitat: Under rocks of middle and lower intertidal zones (Menzies 1952), on buoys from the surface to 1.8 m (Miller 1968). The figured specimen was collected from a within a decayed float with the shipworm, *Bankia setacea*.

Salinity: Collected at a salinity of 30.

Temperature: Apparently not adaptable to extreme temperatures (compare to *I. k. kincaidi* Miller 1968).

Tidal Level: Middle and lower intertidal zones (Menzies 1952) ranging from surface to 1.8 m deep (Miller 1968). The figured specimen was collected near the water line.

Associates: The shipworm, *Bankia setacea* and harpacticoid copepods.

Abundance: Fairly common in wood debris with *Bankia setacea*.

Life-History Information

Reproduction: Most isopods have separate sexes (i.e. dioecious, Brusca and Iverson 1985) (although protogynous and protandric species are known, Araujo et al. 2004; Boyko and Wolff 2014). Reproduction proceeds by copulation and internal fertilization where eggs are deposited within a few hours after copulation and brooded within the female marsupium (Brusca and Iverson 1985). The biphasic molting of isopods allows for copulation; the posterior portion of the body molts and individuals mate, then the anterior portion, which holds the brood pouch, molts (Sadro 2001). Embryonic development proceeds within the brood chamber and is direct with individuals hatching as manca larvae that resemble small adults, with no larval stage (Boyko and Wolff 2014). Oviparous *I. derjugini* were collected in February, May and June (northern California, Menzies 1952).

Larva: Since most isopods are direct developing, they lack a definite larval stage. Instead this young developmental stage resembles small adults (e.g. Fig. 40.1, Boyko and Wolff 2014). Most isopods develop from embryo to a manca larva, consisting of three stages. Manca larvae are recognizable by lacking the seventh pair of pereopods, but otherwise resemble small adults. They usually hatch from the female marsupium at the second stage and the molt from second to

third manca produces the seventh pair of pereopods and sexual characteristics (Boyko and Wolff 2014). Isopod development and larval morphology can vary between groups (e.g. Gnathiidae, Cryptoniscoidea, Bopyroidae, Cymothoidae, Oniscoidea) (see Boyko and Wolff 2014). Parasitic isopods, for example, have larvae that are morphologically dissimilar from adults (Sadro 2001). Isopod larvae are not common members of the plankton, with parasitic larvae most likely to be observed. Occasionally, suspended benthic juveniles or pelagic species are collected in plankton samples, but these can be differentiated from larvae by their larger size (Sadro 2001).

Juvenile:

Longevity:

Growth Rate: Growth among isopods occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007), however, isopods do not autotomize limbs as readily as other groups (Brusca and Iverson 1985). Compared to other arthropods, isopods exhibit a unique biphasic molting, in which the posterior 1/2 of the body molts before the anterior 1/2 (Brusca et al. 2007).

Food:

Predators: Isopods play a significant role as intermediate food web links, like amphipods, (e.g. see *Americorophium salmonis*, this guide) that are consumed by more than 20 species of marine fish (Welton and Miller 1980; cabezon, Best and Stachowicz 2012) and whales (Brusca et al. 2007).

Behavior:

Bibliography

1. ARAUJO, P. B., A. F. QUADROS, M. M. AUGUSTO, and G. BOND-BUCKUP. 2004. Postmarsupial development of *Atlantoscia floridana* (van Name, 1940) (Crustacea, Isopoda, Oniscoidea): sexual differentiation and size at onset of sexual maturity. *Invertebrate Reproduction and Development*. 45:221-230.
2. BEST, R. J., and J. J. STACHOWICZ. 2012. Trophic cascades in seagrass meadows depend on mesograzers

variation in feeding rates, predation susceptibility, and abundance. *Marine Ecology Progress Series*. 456:29-42.

3. BOYKO, C. B., and C. WOLFF. 2014. Isopoda and Tanaidacea, p. 210-215. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
4. BRANDT, A., and G. C. B. POORE. 2003. Higher classification of the flabelliferan and related isopoda based on a reappraisal of relationships. *Invertebrate Systematics*. 17:893-923.
5. BRUSCA, R. C., C. R. COELHO, and S. TAITI. 2007. Isopoda, p. 503-541. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
6. BRUSCA, R. C., and E. W. IVERSON. 1985. A guide to the marine isopod crustacea of Pacific Costa Rica. *Revista de Biología Tropical*. 33:1-77.
7. HATCH, M. H. 1947. The Chelifera and isopoda of Washington and adjacent regions. *University of Washington Publications in Biology*. 10:155-274.
8. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
9. LINSE, K., J. A. JACKSON, M. V. MALYUTINA, and A. BRANDT. 2014. Shallow-water northern hemisphere *Jaera* (Crustacea, Isopoda, Janiridae) found on whale bones in the southern ocean deep sea: ecology and description of *Jaera tyleri* sp. nov. *Plos One*. 9:1-20.
10. MENZIES, R. J. 1952. Some marine asellote isopods from northern California, with descriptions of nine new species. *Proceedings of the United States National Museum*. 102:117-159.
11. MILLER, M. A. 1968. Isopoda and Tanaidacea from buoys in coastal waters of the continental United States, Hawaii, and the Bahamas (Crustacea). *Proceedings of the*

- United States National Museum.
125:1-53.
12. —. 1975. Phylum Arthropoda: Crustacea, Tanaidacea and Isopoda, p. 277-312. *In*: Light's manual: intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
 13. RICHARDSON, H. 1905. Monograph on the isopods of North America. Bulletin of the United States Natural Museum. 54:727.
 14. SADRO, S. 2001. Arthropoda: Decapoda, p. 176-178. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 15. WELTON, L. L., and M. A. MILLER. 1980. Isopoda and Tanaidacea: the isopods and allies, p. 536-558. *In*: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 16. WILSON, G. D. F. 1994. A phylogenetic analysis of the isopod family Janiridae (Crustacea). Invertebrate Taxonomy. 8:749-766.
 17. WILSON, G. D. F., and J. WAEGELE. 1994. Review of the family Janiridae (Crustacea: Isopoda: Asellota). Invertebrate Taxonomy. 8:683-747.

Updated 2015

Ligia pallasii

A rock louse or shore isopod

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Isopoda, Oniscidea
Family: Ligiidae

Taxonomy: The genus *Ligia* was very briefly called *Ligyda* in the early 1900s. Since then, the genus has been split into four genera (*Geoligia*, *Megaligia*, *Nesoligia* and *Ligia*) based on morphological characters (e.g. antennulae, mouthparts, telson) (Jackson 1927). However, Van Name reduced these genera to subgeneric status and reinstated the genus *Ligia* in 1936 (Brusca 1980). Currently, these subgeneric names are rarely used and, instead, researchers refer to *Ligia pallasii* (e.g. Brusca et al. 2007).

Description

Size: To 35 mm in length (including uropods, which are 3 mm long) and approximately 11 mm wide (Brusca and Brusca 1978). The figured specimen (from Coos Bay) is 22 mm long.

Color: Mottled gray and often brown, with granular surface.

General Morphology: Isopod bodies are dorso-ventrally flattened and can be divided into a compact **cephalon**, with eyes, two **antennae** and **mouthparts**, and a **pereon** (thorax) with eight segments, each bearing similar **pereopods** (hence the name “isopod”). Posterior to the pereon is the **pleon**, or abdomen, with six segments, the last of which is fused with the telson (the **pleotelson**) (see Plate 231, Brusca et al. 2007). The Isopoda can be divided into two groups: ancestral (“short-tailed”) groups (i.e. suborders) that have short telsons and derived (“long-tailed”) groups with long telsons, *L. pallasii* groups among the former (see Fig. 3, Garthwaite and Lawson 1992; Brandt and Poore 2003; Plate 248C, Brusca et al. 2007). The suborder to which *L. pallasii* belongs, Oniscidea, is the largest isopod suborder and the only fully-terrestrial crustacean group (Brusca et al. 2007).

Cephalon: More than twice as wide as long with rounded anterior margin and without lobes (Fig. 1) (family Ligiidae, Brusca et al. 2007).

Rostrum:

Eyes: Large, round, composite, and close to lateral margin (Fig. 1) (Welton and

Miller 1980). Separated in front by twice the length of the eye.

Antenna 1: First antennae are vestigial (Oniscidea, Brusca et al. 2007).

Antenna 2: Second antennae reach to middle of fourth thoracic segment (Fig. 1). The second antennae are with peduncles of five articles: the first two are short, the third is twice as long as the second, the fourth is 1½ x longer than the third, and the fifth 1½ x longer than the fourth (Welton and Miller 1980). The flagellum has 15 articles (Hatch 1947).

Mouthparts: In order from outside of buccal cavity: maxillipeds with palp of five articles (Fig. 8), second maxillae with two plumose processes on inner side of lobe (Fig. 5), first maxillae with three plumose processes on the inner lobe (Fig. 4), and the mandible with large, broad molar surfaces, and no palp (Fig. 3).

Pereon: First segment fused with head followed by seven free pereonites. Contains a tubular heart and cardiac ganglion consisting of six neurons (see Fig. 1, Sakurai and Wilkens 2003).

Pereonites: First four pereonites are subequal, last three are somewhat shorter along medial line and extend downward laterally. Epimera (flattened lateral extensions to pereonites) form broad plates, especially in males (Figs. 1, 4).

Pereopods: Seven pairs of delicate walking legs. Carpus and merus of first pair is swollen and not grooved (Hatch 1947).

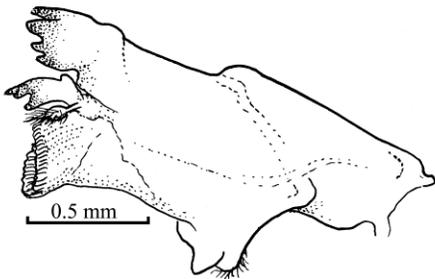
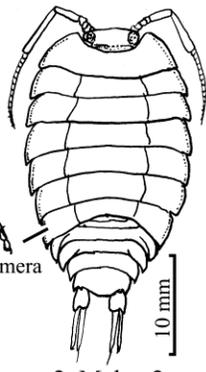
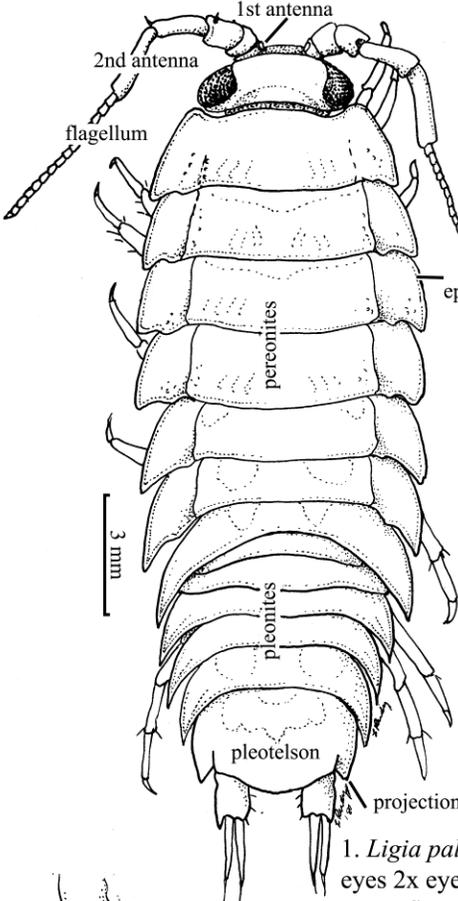
Pleon: Pleon as wide as thorax and with five free pleonites and a short pleotelson (Fig. 1).

Pleonites: First two pleonites narrow and without downwardly extending lateral edges, which mark last three segments (Fig. 1).

Pleopods: Paired breathing appendages beneath pleonites have whitish tissue. Male genitalia, paired but not fused, is present on second pleopods (Fig. 7).

Uropods: Terminal and styliform, with bases about as long as wide. No process at inner distal margin of basal joint (Fig. 6), uropod

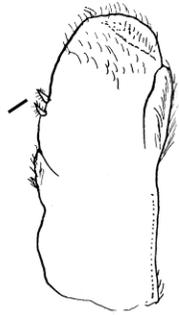
Ligia pallasii



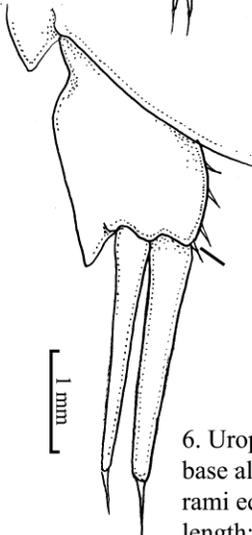
3. Mandible x50:
no palp; broad molar surface.



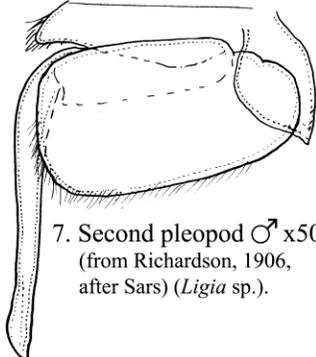
4. First maxilla x50:
three plumose processes,
inner lobe.



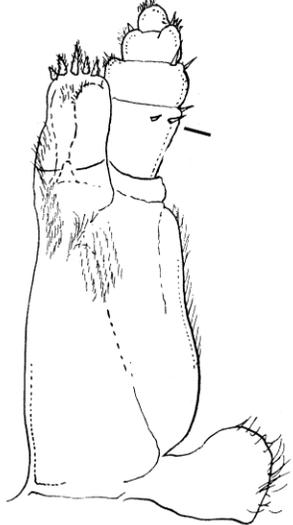
5. Second maxilla x50:
two plumose processes.



6. Uropod x20:
base almost square;
rami equal, 2x base
length; no process on
inner margin.



7. Second pleopod ♂ x50:
(from Richardson, 1906,
after Sars) (*Ligia* sp.).



8. Maxilliped x50:
palp: five articles.

1. *Ligia pallasii* ♀ x8:
eyes 2x eye length
apart; first antennae
vestigial; second: 15
articled flagellum; post-
lateral pleotelson
projections.

rami equal and about twice the length of the peduncle (less than $1/2$ total body length, *Ligia*, Hatch 1947).

Pleotelson: Rounded on middle of posterior edge and postero-lateral projections not quite as long as middle (Fig. 1).

Sexual Dimorphism: Males with penial processes on second **pleopods**, and with wide epimera (Fig. 2). Females, when ovigerous, with oöstegites. Mature males are larger and broader than females (Carefoot 1973a, but see Kozloff 1993).

Possible Misidentifications

The order Isopoda contains 10,000 species, $1/2$ of which are marine and comprise 10 suborders, with eight present from central California to Oregon (see Brusca et al. 2007). Among isopods with small, short telsons, there are several groups (i.e. suborders) including Phreatoicidea, Asellota, Microcerberidea, Calabozoidea and Oniscidea.

The monophyletic Oniscidea (previously part of the paraphyletic Scyphacidae, see Holdrich et al. 1984 in Schmidt 2000, 2002) is a fully-terrestrial group composed of 4,000 described species, with 22 known locally (among 10 families, Schmidt 2002; Brusca et al. 2007). Members are characterized by seven pereonites, the first not fused with the head, seven pairs of pereopods, male penes on the sternum of pereonite seven, a pleotelson that does not curve dorsally, vestigial (or very small) antennules and a pleon with five free pleonites (Brusca et al. 2007). The first and second pleopods are also elongated in males for copulation, many species have a water conducting system and some have respiratory structures on pleopods called pseudotracheae. The Oniscidea can be divided into three major ecological groups: the runners (slender bodies with long pereopods, the clingers (broad bodies with short pereopods) and the rollers (convex bodies that roll into balls) (Schmalfuss 1984 in Brusca et al. 2007). *Ligia pallasii* are fast runners (Brusca 1980).

The Ligiidae are usually littoral, they can swim, but in our area are restricted to the upper littoral (spray) zone (Hatch 1947). They have terminal uropods that are conspicuous dorsally, flagellum antenna with more than 10 articles and eyes with

more than 50 ommatidia each (Brusca et al. 2007). The Ligiidae can further be distinguished from the other oniscidean families by having more than four articles in the flagellum of the second antennae, and by their lack of anterolateral head lobes. This family is represented by four local species, two in the genus *Ligia*, including *L. occidentalis* and *L. pallasii* and two in the genus *Ligidium*, including *L. gracile* and *L. lactum*. The former genus is semi-terrestrial and occurs in higher intertidal marine habitats, while the two latter species occur in riparian habitats (Brusca 1980; Brusca et al. 2007). *Ligidium* species have uropods with processes at the inner distal margin, to articulate the endopod (*Ligia* species do not). The genus *Ligia* is characterized by a pleotelson that bears posterolateral projections (see Fig. 1) and a uropod that has endo- and exopod insertions at the same level (*Ligidium* species lack these projections) (Brusca et al. 2007).

The species closest to *L. pallasii* on the northeastern Pacific shore is *Ligia occidentalis*, an inhabitant mostly of rocky outer shores, which, like *L. pallasii*, is often found near fresh-water seeps (Wilson 1970). It can tolerate greater extremes of dryness than *L. pallasii*. The two species can be distinguished morphologically. *Ligia occidentalis* is narrower than *L. pallasii*, being over twice as long as wide and its eyes that are closer together, about one eye's length apart (Garthwaite and Lawson 1992). Furthermore, its uropod bases are several times longer than broad (*L. pallasii*'s are almost square) (Brusca et al. 2007). Its second antennal flagella are longer, extending to the sixth thoracic segment, and contain 29 articles, not 15. This species occurs on rocky shores, from Oregon south (Brusca et al. 2007).

Ecological Information

Range: Known range includes western Aleutians south to Santa Cruz, California (Welton and Miller 1980). Across this range, there are three distinct clades (mitochondrial COI sequence data) and, within those clades, lower latitudes show greater divergence than those at northern latitudes (Eberl 2013).

Local Distribution: Oregon sites include estuaries at Coos and Depoe Bay and Florence, as well as outer shores (Hatch 1947).

Habitat: Outer shore in deep crevices, under ledges, and near freshwater seepage. Estuarine habitats in hard-packed beaches, pilings, docks, as well as rocks. Individuals cannot tolerate extreme wetting or drying for extended periods and are often found in cool, moist conditions (Wilson 1970), preferring shaded rocky cliffs and caves (Ricketts and Calvin 1952; Eberl 2012) along the open coast (Garthwaite and Lawson 1992). Young individuals prefer moist macroalgae, particularly *Enteromorpha* (Carefoot 1979). Phylogenetically, isopods in the genus *Ligia* are thought to be in evolutionary transition from sea to land environments. Thus, they have a variety of unique physiological traits associated with each habitat (Wilson 1970; Zimmer 2002). The composition of respiratory proteins, hemocyanin present in *L. pallasii* have been described (see Terwilliger 1982).

Salinity: Found in full salt water habitats, but near fresh water seeps. Individuals can osmoregulate well and are found in areas of variable salinity (Wilson 1970). *Ligia pallasii* has been the subject of some toxicity research (e.g. Carefoot 1990a, b).

Temperature: Does not tolerate extended heat or drying, lives permanently in cool moist habitats (Wilson 1970).

Tidal Level: Individuals reported living on cliffs that are 1.5–6 meters above tide level in Moss Beach, California. In estuarine beaches of South Slough in Coos Bay, individuals are found at about 1.5 meters.

Associates: Beach wrack and wood debris associates include isopods *Limnoria*, and amphipods *Orchestia* and *Orchestoidea*. *Ligia* species *L. pallasii* and *L. occidentalis* both host mycoplasma-like symbionts that are believed to have aided in the sea to land transition among the Oniscidea (Eberl 2010).

Abundance: *Ligia pallasii* is the most common *Ligia* species on extreme northern California coast (Brusca and Brusca 1978). Abundant along the open coast from Alaska to San Francisco, California (Kozloff 1993).

Life-History Information

Reproduction: Most isopods have separate sexes (i.e. dioecious, Brusca and Iverson 1985) (although protogynous and protandric species are known, Araujo et al. 2004; Boyko and Wolff 2014). Reproduction proceeds by copulation and internal fertilization where eggs are deposited within a few hours after

copulation and brooded within the female marsupium (Brusca and Iverson 1985). The biphasic molting of isopods allows for copulation; the posterior portion of the body molts and individuals mate, then the anterior portion, which holds the brood pouch, molts (Sadro 2001). Embryonic development proceeds within the brood chamber and is direct with individuals hatching as manca larvae that resemble small adults, with no larval stage (Boyko and Wolff 2014). Gravid *L. pallasii* females have been observed year-round (Ecola State Park, Oregon to Ventura California, Eberl 2012). Females are found with young in early spring through summer (April to May) in Coos Bay and females with broods were collected in July in Mora, Washington (Ricketts and Calvin 1952). The average brood size is 48 ± 11 (Carefoot 1973a; Welton and Miller 1980).

Larva: Since most isopods are direct developing, they lack a definite larval stage. Instead this young developmental stage resembles small adults (e.g. Fig. 40.1, Boyko and Wolff 2014). Most isopods develop from embryo to a manca larva, consisting of three stages. Manca larvae are recognizable by lacking the seventh pair of pereopods, but otherwise resemble small adults. They usually hatch from the female marsupium at the second stage and the molt from second to third manca produces the seventh pair of pereopods and sexual characteristics (Boyko and Wolff 2014). Isopod development and larval morphology can vary between groups (e.g. Gnathiidae, Cryptoniscoidea, Bopyroidae, Cymothoidae, Oniscoidea) (see Boyko and Wolff 2014). Parasitic isopods, for example, have larvae that are morphologically dissimilar from adults (Sadro 2001). Isopod larvae are not common members of the plankton, and parasitic larvae are most likely to be observed. Occasionally, suspended benthic juveniles or pelagic species are collected in plankton samples, but these can be differentiated from larvae by their larger size (Sadro 2001).

Juvenile: Young individuals are approximately 2–5 mm in length after release from the female brood pouch (Carefoot 1979). Individuals reach sexual maturity after one year (Carefoot 1973a).

Longevity: 1.5–2 years (Carefoot 1973a; Welton and Miller 1980).

Growth Rate: Growth among isopods occurs in conjunction with molting where the

exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autonomized (Kuris et al. 2007), however, isopods do not autotomize limbs as readily as other groups (Brusca and Iverson 1985). Compared to other arthropods, isopods exhibit a unique biphasic molting, in which the posterior 1/2 of the body molts before the anterior 1/2 (Brusca et al. 2007). The hemolymph ion composition of *L. pallasii* has been documented throughout several molting stages and concentrations of Ca²⁺ and K⁺ changed most significantly over the course of a a molt (Siegler et al. 2000).

Food: A scavenger, feeding mostly on decayed algal material as well as animal detritus (Kozloff 1993; Brusca and Brusca 1978). Individuals showed preference to aged and decaying beach wrack over fresh macroalgae of the same species (Pennings et al. 2000). Food gathering is restricted to cool, humid periods (Wilson 1970) and includes diatoms, insect larvae and macro algae (e.g. *Ulva* sp., *Nereocystis leutkeana*) (Carefoot 1973b). With a daily energy budget of about 14 J per 250 mg per isopod, *L. pallasii* individuals require at least 11 mg of seaweed to survive, which takes about 35 minutes to ingest (Carefoot et al. 2003).

Predators: Birds, humans (e.g. for fish bait) and *Pachygrapsus crassipes* (Welton and Miller 1980). Isopods play a significant role as intermediate food web links, like amphipods, (e.g. see *Americorophium salmonis*, this guide) that are consumed by more than 20 species of marine fish (Welton and Miller 1980; cabezon, Best and Stachowicz 2012) and whales (Brusca et al. 2007).

Behavior: Uropod rami are dipped into pools to obtain moisture for gills (pleopods) (Brusca and Brusca 1978). The energy budget of *L. pallasii* can be divided as follows: 0.56 J for resting, 1.36 J for feeding, 1.31 J for running, 0.96 J for molting and 0.57 J per 250 mg per individual per hour for brood-carrying (Carefoot et al. 2003)

Bibliography

1. ARAUJO, P. B., A. F. QUADROS, M. M. AUGUSTO, and G. BOND-BUCKUP. 2004. Postmarsupial development of *Atlantoscia floridana* (van Name, 1940) (Crustacea, Isopoda, Oniscidea): sexual differentiation and size at onset of sexual maturity. *Invertebrate Reproduction and Development*. 45:221-230.
2. BEST, R. J., and J. J. STACHOWICZ. 2012. Trophic cascades in seagrass meadows depend on mesograzers: variation in feeding rates, predation susceptibility, and abundance. *Marine Ecology Progress Series*. 456:29-42.
3. BOYKO, C. B., and C. WOLFF. 2014. Isopoda and Tanaidacea, p. 210-215. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
4. BRANDT, A., and G. C. B. POORE. 2003. Higher classification of the flabelliferan and related isopoda based on a reappraisal of relationships. *Invertebrate Systematics*. 17:893-923.
5. BRUSCA, G. J., and R. C. BRUSCA. 1978. A naturalist's seashore guide. Mad River Press, Arcata, CA.
6. BRUSCA, R. C. 1980. Common intertidal invertebrates of the Gulf of California. University of Arizona Press, Tucson.
7. BRUSCA, R. C., C. R. COELHO, and S. TAITI. 2007. Isopoda, p. 503-541. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
8. BRUSCA, R. C., and E. W. IVERSON. 1985. A guide to the marine isopod crustacea of Pacific Costa Rica. *Revista de Biología Tropical*. 33:1-77.
9. CAREFOOT, T. H. 1973a. Feeding, food preference, and uptake of food energy by supralittoral isopod *Ligia pallasii*. *Marine Biology*. 18:228-236.
10. —. 1973b. Studies on growth, reproduction, and life cycle of supralittoral isopod *Ligia pallasii*. *Marine Biology*. 18:302-311.
11. —. 1979. Microhabitat preferences of young *Ligia pallasii* Brandt (Isopoda). *Crustaceana*. 36:209-214.
12. —. 1990a. Specific dynamic action (SDA) in the supralittoral isopod, *Ligia pallasii*: effect of ration and body size on SDA. *Comparative Biochemistry*

- and Physiology a-Physiology. 95:317-320.
13. —. 1990b. Specific dynamic action (SDA) in the supralittoral isopod, *Ligia pallasii*: identification of components of apparent SDA and effects of dietary amino acid quality and content on SDA. Comparative Biochemistry and Physiology a-Physiology. 95:309-316.
 14. CAREFOOT, T. H., B. E. TAYLOR, and K. BRETT. 1998. A day in the life of an isopod: time and energy allocations in the semiterrestrial *Ligia pallasii*. Israel Journal of Zoology. 44:463-471.
 15. EBERL, R. 2010. Sea-land transitions in isopods: pattern of symbiont distribution in two species of intertidal isopods *Ligia pallasii* and *Ligia occidentalis* in the Eastern Pacific. Symbiosis. 51:107-116.
 16. —. 2012. Distribution, habitat and food preferences of sympatric high intertidal isopod species *Ligia occidentalis* and *Ligia pallasii* (Ligiidae: Oniscidea). Journal of Natural History. 46:1779-1797.
 17. —. 2013. Phylogeography of the high intertidal isopod *Ligia pallasii* Brandt, 1833 (Isopoda: Oniscidea) from the Aleutian Islands to Monterey Bay. Journal of Crustacean Biology. 33:253-264.
 18. GARTHWAITE, R. L., and R. LAWSON. 1992. Oniscidea isopoda of the San Francisco Bay area. Proceedings of the California Academy of Sciences. 47:303-328.
 19. HATCH, M. H. 1947. The Chelifera and isopoda of Washington and adjacent regions. University of Washington Publications in Biology. 10:155-274.
 20. JACKSON, H. G. 1927. A new subgenus of *Ligia*, with further observations on the genus. Annals & Magazine of Natural History. 19:129-136.
 21. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 22. MILLER, M. A. 1938. Comparative ecological studies on the terrestrial isopod crustacea of the San Francisco Bay region. University of California (Berkeley) Publications in Zoology. 41:165-172.
 23. PENNING, S. C., T. H. CAREFOOT, M. ZIMMER, J. P. DANKO, and A. ZIEGLER. 2000. Feeding preferences of supralittoral isopods and amphipods. Canadian Journal of Zoology. 78:1918-1929.
 24. RICHARDSON, H. 1906. Descriptions of new Isopod crustaceans of the family Sphaeromidae. Washington DC Smithsonian Institution U S National Museum Proceedings. 31:(1-22).
 25. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
 26. SADRO, S. 2001. Arthropoda: Decapoda, p. 176-178. In: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 27. SAKURAI, A., and J. L. WILKENS. 2003. Tension sensitivity of the heart pacemaker neurons in the isopod crustacean *Ligia pallasii*. Journal of Experimental Biology. 206:105-115.
 28. SCHMIDT, C. 2000. Revision of *Detonella* Lohmander, 1927 (Crustacea, Isopoda, Oniscidea). Mitteilungen aus dem Museum fuer Naturkunde in Berlin Zoologische Reihe. 76:51-60.
 29. —. 2002. Contribution to the phylogenetic system of the Crinocheta (Crustacea, Isopoda). Part 1. (Olibrinidae to Scyphacidae s. str.). Mitteilungen aus dem Museum fuer Naturkunde in Berlin Zoologische Reihe. 78:275-352.
 30. TERWILLIGER, N. B. 1982. Effect of subunit composition on quaternary structure of isopod (*Ligia pallasii*) hemocyanin. Biochemistry. 21:2579-2586.
 31. WELTON, L. L., and M. A. MILLER. 1980. Isopoda and Tanaidacea: the isopods and allies, p. 536-558. In: Intertidal invertebrates of California. R.

- H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
32. WILSON, W. J. 1970. Osmoregulatory capabilities in isopods: *Ligia occidentalis* and *Ligia pallasii*. *Biological Bulletin*. 138:96-108.
 33. ZIEGLER, A., T. GROSPIETSCH, T. H. CAREFOOT, J. P. DANKO, M. ZIMMER, I. ZERBST-BOROFFKA, and S. C. PENNING. 2000. Hemolymph ion composition and volume changes in the supralittoral isopod *Ligia pallasii* Brandt, during molt. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*. 170:329-336.
 34. ZIMMER, M. 2002. Nutrition in terrestrial isopods (Isopoda: Oniscidea): an evolutionary-ecological approach. *Biological Reviews*. 77:455-493.

Updated 2015

Limnoria tripunctata

A gribble

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Isopoda; Flabellifera
Family: Limnoriidae

Taxonomy: *Limnoria* was described in 1813 by Leach and has been placed in a variety of isopod families since (e.g. Asellidae), until Harger erected the family Limnoriidae for it, in 1880 (Menzies 1957). It was divided into two subgenera on the basis of boring substrate and associated mouthparts (Cookson 1991). *Limnoria Limnoria* were the wood-borers while *Limnoria Phycolimnoria* were the algae-borers (Menzies 1957; Brusca 1980). Thus, *Limnoria Limnoria tripunctata* is sometimes seen, although these subgeneric names are rarely used today (Cookson 1991; Brusca et al. 2007).

Description

Size: Limnoriids are small and *L. tripunctata* is no exception, reaching maximum lengths of 2.5 mm.

Color: Light tan, whitish and often encrusted with debris.

General Morphology: Isopod bodies are dorso-ventrally flattened and can be divided into a compact **cephalon**, with eyes, two **antennae** and **mouthparts**, and a **pereon** (thorax) with eight segments, each bearing similar **pereopods** (hence the name “isopod”). Posterior to the pereon is the **pleon**, or abdomen, with six segments, the last of which is fused with the telson (the **pleotelson**) (see Plate 231, Brusca et al. 2007). The Isopoda can be divided into two groups: ancestral (“short-tailed”) groups (i.e. suborders) that have short telsons and derived (“long-tailed”) groups with long telsons. Members of the Flabellifera, to which *L. tripunctata* belongs, fall into the long-tailed variety (see Fig. 86, Kozloff 1993). *Limnoria tripunctata* individuals are able to roll into a ball and are easily recognizable by their small size and wood-boring habits (Brusca 1980).

Cephalon: Smooth, rounded and modified for boring (Fig. 1).

Rostrum:

Eyes: Lateral and anterior (Fig. 1).

Antenna 1: First antenna flagellum with four articles and peduncle with three (Fig. 3). Both antennae are reduced, separated at

midline, and positioned in a nearly transverse line (Fig. 1).

Antenna 2: Second antenna flagellum with five articles (Fig. 4).

Mouthparts: Mandibles with file-like ridges (right) and rasping surface (left), but lack *lacina mobilis* and molar processes (Brusca 1980).

Pereon:

Pereonites: Seven total segments, the first of which is widest (Figs. 1, 2) and coxal plates are present on pereonites 2–7 (Brusca 1980).

Pereopods: In mature females, leaf-like ooestegites are present at the base of each of first four pairs of legs and forms a brood pouch or marsupium (see Fig. 6, *Corophiurn spinicorne*, this guide).

Pleon:

Pleonites: Five free pleonites with fifth somite bearing three tubercles (Fig. 1).

Pleopods:

Uropods: Uropod branches dissimilar, with short and claw-like exopod and long, apically blunt endopod (Fig. 6).

Pleotelson: Ornamented pleotelson with three anterior tubercles (“*tri-punctata*”, Fig. 1) and tuberculate posterior and lateral borders (Fig. 5).

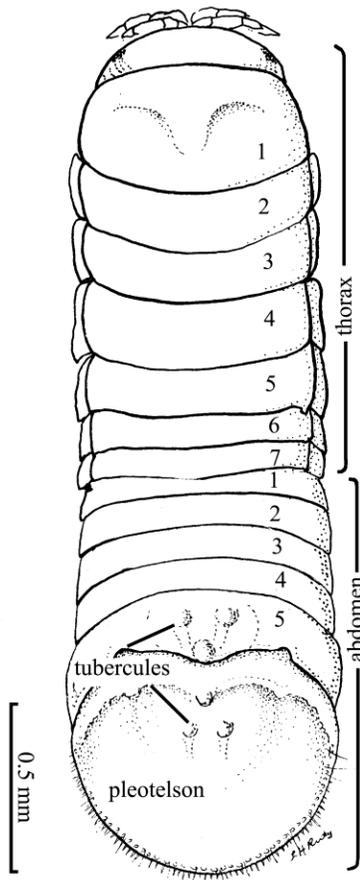
Sexual Dimorphism: Mature females are conspicuous with a marsupium (see **pereopods**) and males with modified posterior end of the seventh pereonite (see Fig. 1, Menzies 1972).

Possible Misidentifications

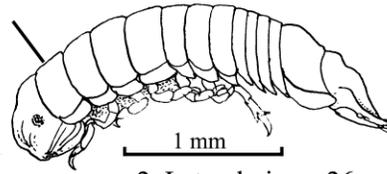
The order Isopoda contains 10,000 species, 1/2 of which are marine and comprise 10 suborders, with eight present from central California to Oregon (see Brusca et al. 2007). Among isopods with elongated telsons (with anuses and uropods that are subterminal), there are several groups (i.e. suborders) including the Valvifera, Anthuridea, Gnathiidea, Epicaridea and Flabellifera.

The Flabellifera is a large assemblage and contains 3,000 species with seven families occurring locally, three

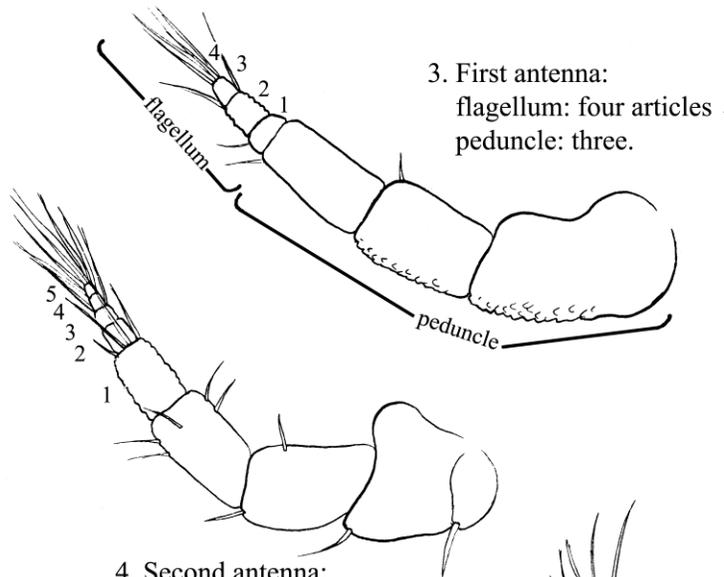
Limnoria tripunctata



1. *Limnoria tripunctata* (L:2.5mm) x56:
head smooth; antennae reduced, transverse;
fifth abdominal somite: three tubercles;
telson: three tubercles.

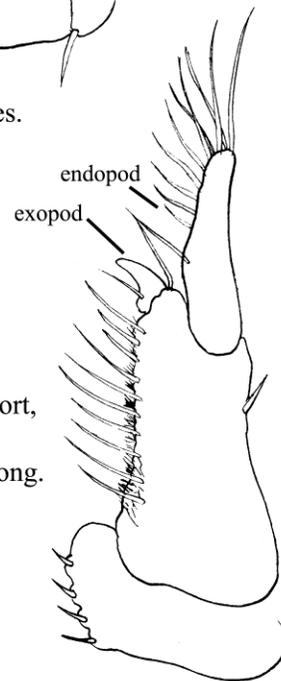


2. Lateral view x26:
eyes lateral; head rounded for boring;
first thoracic segment widest.



3. First antenna:
flagellum: four articles
peduncle: three.

4. Second antenna:
flagellum: five articles.



6. Uropod:
exopod short,
claw-like;
endopod long.



5: Pleotelson:distal border:
small tubercles.

of which are not present north of Point Conception, California (Brusca et al. 2007). Limnoriids are wood-boring species that are characterized by reduced uropods, small exopods, and a body that is less than 4 mm in length (see Brusca et al. 2007 for other distinguishing characters). This family comprises only four local species (70 described worldwide) and all are in the genus *Limnoria*.

Limnoria algarum, bores in algal holdfasts, not wood, and is the only species with a simple incisor mandibular process, lacking a file that is present in the other three, wood-boring, species. *Limnoria lignorum* has a pleotelson with dorsal surface that forms a Y-shaped keel at the base while *L. quadripunctata* and *L. tripunctata* have pleotelsons with symmetrically arranged anterior tubercles. The two latter species can be differentiated (as their names suggest) by the number of tubercles present, four in *L. quadripunctata* and three in *L. tripunctata* (Brusca et al. 2007).

Ecological Information

Range: Type locality is San Diego, California. Known range from Atlantic and Pacific coasts in temperate and tropical waters and capable of interbreeding over large geographic distances (Menzies 1972) within a temperature range of 15–30°C (44° to 12° N) (Beckman and Menzies 1960).

Limnoria tripunctata is a well-established species in European coastal waters (Borges et al. 2014).

Local Distribution: Oregon distribution in upper bays including Coos, Yaquina, Tillamook estuaries.

Habitat: Docks and pilings, chiefly in bays and estuaries, where it burrows into wood, whether it is floating or submerged (Johnson and Menzies 1956). The wood serves as both food and protection. *Limnoria tripunctata* is even undeterred by creosote preserved wood (Menzies 1951; Ricketts and Calvin 1952; Borges et al. 2014) (see also **Food**). Within the wood, burrows are equal in diameter throughout and have smooth walls (Sleeter and Coull 1973). Bite marks left on wood by *Limnoria* species are distinct and measure 50–80 µm in diameter and tunnels reach depths of 2 cm (Pitman et al. 1997). They can completely bury themselves within wood in 4–6 days, but remain close to the wood surface (Ricketts and Calvin 1952).

Salinity: A stenohaline species (Borges et al. 2014) that tolerates salinity and oxygen fluctuations as individuals occur in warm, often salty upper bays. The ideal salinity range is 30–34 (in the lab, Borges et al. 2009), but individuals tolerate salinities from 12 to 48 (Menzies 1972). Other *Limnoria* species (e.g. *L. lignorum*) can't tolerate low salinity (15) or dissolved oxygen content below 1.6 ppm. *Limnoria tripunctata* can stand periodic oxygen depletion, however, (Menzies 1957) and has been observed at salinities of 12 near San Francisco, California, and can survive at salinities between 10–18. However, even *L. tripunctata* cannot survive exposure to freshwater for greater than one day (Menzies 1957).

Temperature: Temperature range from 15° to 30°C (Beckman and Menzies 1960; Menzies 1972; Borges et al. 2009). Highest reproductive rates were observed between 20–25°C, reproduction is impaired below 10°C and egg production takes twice as long at 15°C than at 20°C (Menzies 1957, 1972).

Tidal Level: A shallow water species, *L. tripunctata* occurs from the water surface to 18 meters deep. Individuals prefer lower depths when surface salinity is low or tidal fluctuation is great. Individuals tend to prefer estuary benthos, and commonly occur at the bases of pilings.

Associates: *Limnoria* burrows can be inhabited by the commensal isopod, *Caecijaera*; the sphaeromatid isopod, *Gnorimosphaeroma*; the amphipod, *Chelura*; and the copepod *Donsiella* (Menzies 1957), none of which are borers. The boring mollusk, *Teredo*, can also co-occur in wood where *Limnoria* burrows. After 4–6 months submerged (suspended 1–4 meters above the bottom), untreated wood with *L. tripunctata* developed a community consisting of turbellarians, nematodes, the archiannelid *Dinophilus*; the polychaete *Polydora*; the tanaid, *Leptocheilia savignyi*; copepods and amphipods (Sleeter and Coull 1973). The heterotrich ciliate *Microfolliculina limnoriae*, attaches to the dorsal surface of the pleotelson (up to four individuals per single *L. tripunctata*). The presence of this obligate ciliate may reduce feeding rate and negatively affect swimming, suggesting that this relationship is a form of ectoparasitism (Delgery et al. 2006).

Abundance: The small size of individuals in this genus allows for hundreds to co-occur in a single square inch of wood.

Life-History Information

Reproduction: Most isopods have separate sexes (i.e. dioecious, Brusca and Iverson 1985) (although protogynous and protandric species are known, Araujo et al. 2004; Boyko and Wolff 2014). Reproduction proceeds by copulation and internal fertilization where eggs are deposited within a few hours after copulation and brooded within the female marsupium (Brusca and Iverson 1985). The biphasic molting of isopods allows for copulation; the posterior portion of the body molts and individuals mate, then the anterior portion, which holds the brood pouch, molts (Sadro 2001). Embryonic development proceeds within the brood chamber and is direct with individuals hatching as manca larvae that resemble small adults, with no larval stage (Boyko and Wolff 2014).

Limnoria species exhibit low fecundity, iteroparity and direct development (Menzies 1972) and females in the genus only carry an average of about 9–10 eggs and breeding occurs year-round (Ricketts and Calvin 1952). Adult *L. tripunctata* occur and copulate as pairs within tunnels (see Fig. 2, Menzies 1972) and eggs require 2–4 weeks for development (Borges et al. 2014). Females can produce up to three broods per year, and the number of gravid females in a single population is highest when water temperatures are between 17 and 19°C (Johnson and Menzies 1956). Locally, peak breeding time for *L. tripunctata* is from April to May (Friday Harbor, WA, Welton and Miller 1980) and the average number of eggs per female is 22 (Welton and Miller 1980). Development time from egg deposition to hatching is 17 days (at 20 °C), 15 days (at 22°C), 13 days (at 26°C), 11 days (at 30°C but numbers greatly reduced) (Eltringham 1967).

Larva: Since most isopods are direct developing, they lack a definite larval stage. Instead this young developmental stage resembles small adults (e.g. Fig. 40.1, Boyko and Wolff 2014). Most isopods develop from embryo to a manca larva, consisting of three stages. Manca larvae are recognizable by lacking the seventh pair of pereopods, but otherwise resemble small adults. They usually hatch from the female marsupium at

the second stage and the molt from second to third manca produces the seventh pair of pereopods and sexual characteristics (Boyko and Wolff 2014). Isopod development and larval morphology can vary between groups (e.g. Gnathiidae, Cryptoniscoidea, Bopyroidae, Cymothoidae, Oniscoidea) (see Boyko and Wolff 2014). Parasitic isopods, for example, have larvae that are morphologically dissimilar from adults (Sadro 2001). Isopod larvae are not common members of the plankton, with parasitic larvae most likely to be observed. Occasionally, suspended benthic juveniles or pelagic species are collected in plankton samples, but these can be differentiated from larvae by their larger size (Sadro 2001). Newly hatched *Limnoria* larvae do not swim, but develop this trait over time (Ricketts and Calvin 1952).

Juvenile:

Longevity: There is some evidence that individuals leave their burrows and dig separate “tombs” into which they settle to die (Sleeter and Coull 1973).

Growth Rate: Growth among isopods occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007), however, isopods do not autotomize limbs as readily as other groups (Brusca and Iverson 1985). Compared to other arthropods, isopods exhibit a unique biphasic molting, in which the posterior 1/2 of the body molts before the anterior 1/2 (Brusca et al. 2007). Intermolt period is 25 days in *L. tripunctata*, but decreases with time and age of individual (Ria Formosa, Portugal, Delgery et al. 2006). See Fig. 4 Johnson and Menzies 1956 for plot of seasonal chart of growth rate.

Food: *Limnoria tripunctata* is an economically significant species due to its ability to alter wooden structures by burrowing and ingesting wood (e.g. Fig. 1 Menzies 1957). They use wood as their primary carbon source by producing lignocellulose digesting enzymes (Borges et al. 2014) and, interestingly, have digestive systems void of the microorganisms that aid in digestion of wood and cellulose among other metazoans (Boyle and Mitchell 1978; Sleeter et al. 1978). However, epiphytic bacteria ingested with wood may serve as nutritionally beneficial to species with nitrogen-poor wood diets

(Zachary and Colwell 1979; Zachary et al. 1983; Cragg et al. 1999). Digestion occurs rapidly (8 minutes total, Ricketts and Calvin 1952). The wood-boring ability of limnoriids has instigated research toward alternative structures that deter boring (e.g. Borges et al. 2009; Cragg et al. 1999). *Limnoria tripunctata* is apparently undeterred by creosote preserved wood (Menzies 1951) and populations that ingest creosote wood appear to possess a microbial gut flora unlike those that ingest untreated wood (Zachary and Colwell 1979; Zachary et al. 1983). *Limnoria tripunctata* may represent a resistant strain of gribble, which developed in response to creosote (Welton and Miller 1980). Furthermore, *L. tripunctata* is also reported to tunnel into wood treated with copper chrome arsenic (Pitman et al. 1997).

Predators: Isopods play a significant role as intermediate food web links, like amphipods, (e.g. see *Americorophium salmonis*, this guide) that are consumed by more than 20 species of marine fish (Welton and Miller 1980; cabezon, Best and Stachowicz 2012), whales (Brusca et al. 2007) and other invertebrates (e.g. polychaete worms, Reish 1954; Brusca 1980).

Behavior: Dispersal between wood habitats occurs by swimming and crawling in young adults. In *Teredo* species, dispersal is by larvae only, adults burrow but do not swim or crawl.

Bibliography

1. ARAUJO, P. B., A. F. QUADROS, M. M. AUGUSTO, and G. BOND-BUCKUP. 2004. Postmarsupial development of *Atlantoscia floridana* (van Name, 1940) (Crustacea, Isopoda, Oniscidea): sexual differentiation and size at onset of sexual maturity. *Invertebrate Reproduction and Development*. 45:221-230.
2. BECKMAN, C., and R. J. MENZIES. 1960. The relationship of reproductive temperature and the geographical range of the marine woodborer *Limnoria tripunctata*. *Biological Bulletin*. 118:9-16.
3. BEST, R. J., and J. J. STACHOWICZ. 2012. Trophic cascades in seagrass meadows depend on mesograzers: variation in feeding rates, predation susceptibility, and abundance. *Marine Ecology Progress Series*. 456:29-42.
4. BORGES, L. M. S., S. M. CRAGG, and S. BUSCH. 2009. A laboratory assay for measuring feeding and mortality of the marine wood borer *Limnoria* under forced feeding conditions: A basis for a standard test method. *International Biodeterioration & Biodegradation*. 63:289-296.
5. BORGES, L. M. S., L. M. MERCKELBACH, and S. M. CRAGG. 2014. Biogeography of wood-boring crustaceans (Isopoda: Limnoriidae) established in European coastal waters. *Plos One*. 9.
6. BOYKO, C. B., and C. WOLFF. 2014. Isopoda and Tanaidacea, p. 210-215. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
7. BOYLE, P. J., and R. MITCHELL. 1978. Absence of microorganisms in crustacean digestive tracts. *Science*. 200:1157-1159.
8. BRUSCA, R. C. 1980. Common intertidal invertebrates of the Gulf of California. University of Arizona Press, Tucson.
9. BRUSCA, R. C., C. R. COELHO, and S. TAITI. 2007. Isopoda, p. 503-541. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
10. BRUSCA, R. C., and E. W. IVERSON. 1985. A guide to the marine isopod crustacea of Pacific Costa Rica. *Revista de Biologia Tropical*. 33:1-77.
11. COOKSON, L. J. 1991. Australasian species of Limnoriidae (Crustacea: Isopoda). *Memoirs of the Museum of Victoria*. 52:137-262.
12. CRAGG, S. M., A. J. PITMAN, and S. M. HENDERSON. 1999. Developments in the understanding of the biology of marine wood boring crustaceans and in methods of controlling them. *International Biodeterioration & Biodegradation*. 43:197-205.
13. DELGERY, C. C., S. M. CRAGG, S. BUSCH, and E. A. MORGAN. 2006. Effects of the epibiotic heterotrich

- ciliate *Mirofolliculina limnoriae* and of moulting on faecal pellet production by the wood-boring isopods, *Limnoria tripunctata* and *Limnoria quadripunctata*. *Journal of Experimental Marine Biology and Ecology*. 334:165-173.
14. ELTRINGHAM, S. K. 1967. The effects of temperature on the development of *Limnoria* eggs (Isopoda: Crustacea). *Journal of Applied Ecology*. 4:521-529.
 15. JOHNSON, M. W., and R. J. MENZIES. 1956. The migratory habits of the marine gribble *Limnoria tripunctata* Menzies in San Diego Harbor, California. *Biological Bulletin*. 110:54-68.
 16. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 17. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 18. MENZIES, R. J. 1951. *Limnoria* and the premature failure of creosoted marine structures in North America, p. M1-17. *In: Report of the Marine Borer Conference*. United States Naval Civil Engineers Research and Evaluation Lab, Port Hueneme, California.
 19. —. 1957. The marine borer family Limnoriidae (Crustacea, Isopoda). Part 1: Northern and Central America: Systematics, distribution, and ecology. *Bulletin of the Marine Science of the Gulf and Caribbean*. 7:101-200.
 20. —. 1972. Experimental interbreeding between geographically separated populations of marine wood-boring isopod *Limnoria tripunctata* with preliminary indications of hybrid vigor. *Marine Biology*. 17:149-8.
 21. PITMAN, A. J., S. M. CRAGG, and G. DANIEL. 1997. The attack of greenheart (*Ocotea rodiaei* Mez) and creosote treated Douglas fir (*Pseudotsuga menziesii* Mirb.) by *Limnoria tripunctata* Menzies. *Material Und Organismen*. 31:281-291.
 22. REISH, D. J. 1954. Polychaetous annelids as associates and predators of the crustacean woodborer, *Limnoria*. *Wasmann Journal of Biology*. 12:223-226.
 23. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
 24. SADRO, S. 2001. Arthropoda: Decapoda, p. 176-178. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 25. SLEETER, T. D., P. J. BOYLE, A. M. CUNDELL, and R. MITCHELL. 1978. Relationships between marine microorganisms and wood-boring isopod *Limnoria tripunctata*. *Marine Biology*. 45:329-336.
 26. SLEETER, T. D., and B. C. COULL. 1973. Invertebrates associated with marine wood boring isopod, *Limnoria tripunctata*. *Oecologia*. 13:97-102.
 27. WELTON, L. L., and M. A. MILLER. 1980. Isopoda and Tanaidacea: the isopods and allies, p. 536-558. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 28. ZACHARY, A., and R. R. COLWELL. 1979. Gut-associated microflora of *Limnoria tripunctata* in marine creosote-treated wood pilings. *Nature*. 282:716-717.
 29. ZACHARY, A., K. K. PARRISH, and J. D. BULTMAN. 1983. Possible role of marine bacteria in providing the creosote-resistance of *Limnoria tripunctata*. *Marine Biology*. 75:1-8.

Updated 2015

Gnorimosphaeroma insulare

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Isopoda, Flabellifera
Family: Sphaeromatidae

Taxonomy: The genus *Gnorimosphaeroma* was described in 1954 by Menzies with six species including *G. insulare* as well as *G. lutea*, *G. oregonensis*, each a subspecies of *G. oregonensis*, differentiable by pleotelson morphology. Some authors later elevated these two subspecies to species status based on habitat and physiology (e.g. Riegel 1959). Furthermore, *G. insulare* and *G. lutea* were synonymized by Hoestlandt in 1977 and, although some authors (including those for our current, local intertidal guide, Brusca et al. 2007) also consider *G. oregonensis* a synonym of *G. insulare*, others differentiate the two based on habitat: *G. insulare* is strictly marine while *G. insulare* is estuarine (Stanhope et al. 1987).

Description

Size: Males up to 8 mm in length (Miller 1975) and almost twice as long as wide.

Color: White with small black chromatophores.

General Morphology: Isopod bodies are dorso-ventrally flattened and can be divided into a compact **cephalon**, with eyes, two **antennae** and **mouthparts**, and a **pereon** (thorax) with eight segments, each bearing similar **pereopods** (hence the name “isopod”). Posterior to the pereon is the **pleon**, or abdomen, with six segments, the last of which is fused with the telson (the **pleotelson**) (see Fig. 1, Harrison and Ellis 1991; Plate 231, Brusca et al. 2007). The Isopoda can be divided into two groups: ancestral (“short-tailed”) groups (i.e. suborders) that have short telsons and derived (“long-tailed”) groups with long telsons. Members of the Flabellifera, to which *G. insulare* belongs, fall into the long-tailed variety. Body surface in *Gnorimosphaeroma insulare* is smooth and with eight segments from cephalon to pereon. Individuals able to roll into a ball (Sphaeromatidae).

Cephalon: Frontal border smooth (Fig. 3).

Rostrum:

Eyes:

Antenna 1: First antenna longer than second and basal articles are separated by the rostrum (Fig. 3) (see Fig. 4 Hoestlandt, 1977).

Antenna 2: Shorter than first antenna (see Fig. 4 Hoestlandt, 1977).

Mouthparts: Mandible with a palp and maxilliped with four articles. Hairs present on antero-lateral edge of articles 2–4 are less than ½ the length of the article (see Figs. 5–8, Hoestlandt 1977).

Pereon:

Pereonites: Seven free pereonites total.

Pereopods: Seven pereopod pairs. The basis of the first pereopod is hairless and distal extremity with one hair or hairless (Fig. 6).

Pleon: Pleon consists of three parts. The first is concealed under the last pereonite, the second consists of several coalesced pleonites often with partial sutures (Fig. 1), and the third part is the large **pleotelson**.

Pleonites: Only two of three reach the lateral margin, third pleonite is under the second (Figs. 1, 4).

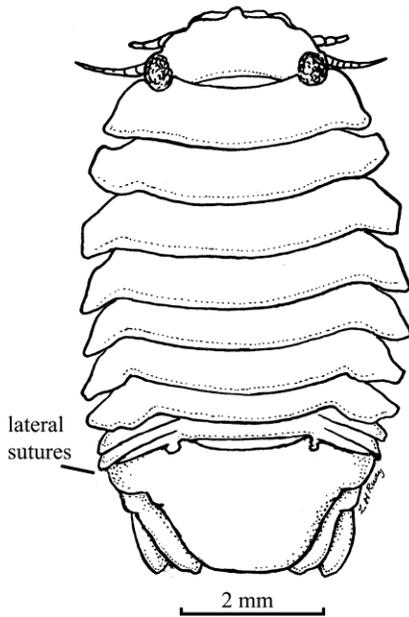
Pleopods: Five pleopod pairs. The first pair is not widely separated at the base, and is similar in size to the second. The first three pairs are with marginal plumose setae. The fourth and fifth pairs are fleshy and without transverse folds, and the fourth is with a bent exopod (Fig. 2, 1-v). The number and arrangement of these folds of the endopods and exopods is considered an important taxonomic character by some authors (e.g. Cassidinidae, Fig. 2, Iverson 1982; Fig. 1, Harrison and Ellis 1991).

Uropods: Two branched uropods visible dorsally, with rigid endopod and flexible exopod (Fig. 5) (see Fig. 9, Hoestlandt 1977).

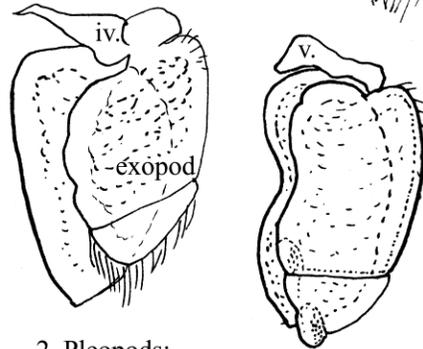
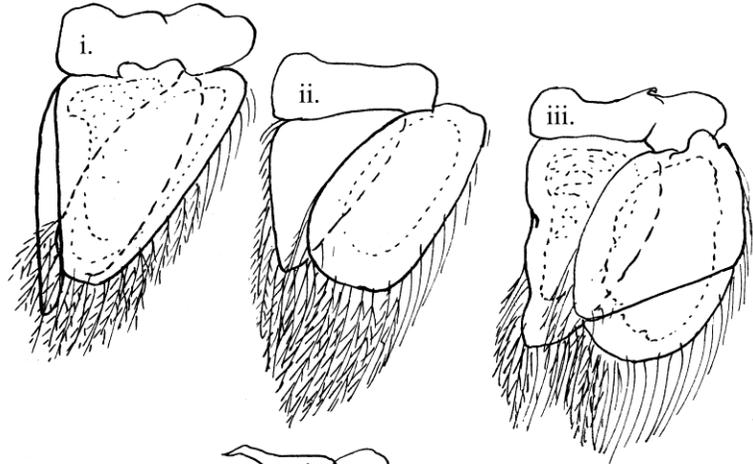
Pleotelson: Rounded and convex (Fig. 1).

Sexual Dimorphism: Conspicuous sexual dimorphism is rare among isopods, however, mature females are often broader and bear a thoracic marsupium while males have modified first pleopods, called gonopods (Sadro 2001; Boyko and Wolff 2014).

Gnorimosphaeroma insulare

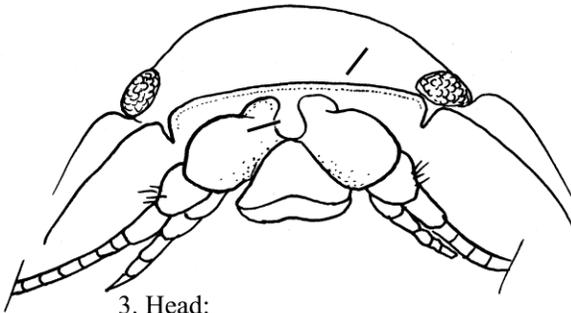


1. *Gnorimosphaeroma insulare* x12.5.



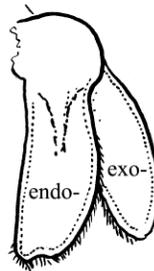
2. Pleopods:

- i, ii similar in size, i not separated at base.
- i, ii, iii with marginal plumose setae.
- iv bent; iv, v fleshy, without transverse folds.



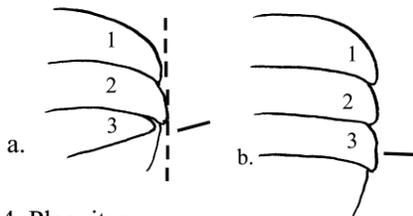
3. Head:

- antennal bases separated by rostrum, frontal border smooth.



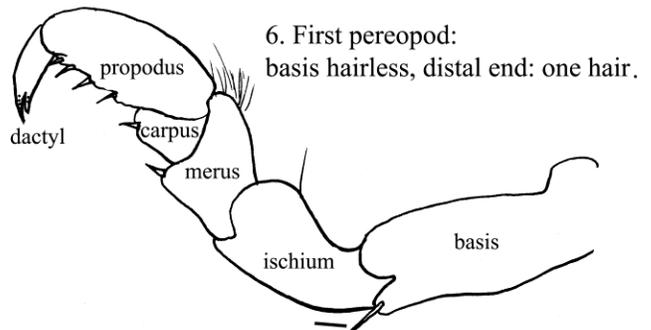
5. Right uropod:

- biramous,
- endopod rigid,
- exopod movable.



4. Pleonites:

- a. two pleonites reach margin, third visible beneath: *G. insulare*.
- b. three pleonites reach lateral margin: *G. oregonense*, *G. rayi*.



6. First pereopod:

- basis hairless, distal end: one hair.

Protogyny has been observed (see **Reproduction**) in *G. insulare* and females can have rudimentary penes after brood release (Brook et al. 1994).

Possible Misidentifications

The order Isopoda contains 10,000 species, 1/2 of which are marine and comprise 10 suborders, with eight present from central California to Oregon (see Brusca et al. 2007). Among isopods with elongated telsons (with anuses and uropods that are subterminal), there are several groups (i.e. suborders) including Valvifera, Anthuridea, Gnathiidea, Epicaridea and Flabellifera.

The Flabellifera is a large assemblage contains 3,000 species with seven families occurring locally, three of which are not present north of Point Conception, California (Brusca et al. 2007). The Flabellifera are characterized by body length that is rarely less than 3 mm and a pleon with less than three free pleonites (plus the pleotelson). The family Sphaeromatidae is almost certainly paraphyletic (Brandt and Poore 2003) and includes 37 species in 11 genera in the western coast of North America (Wall et al. 2015) and has a pleon with 1–2 free pleonites, a convex body that is not depressed, antennae that are widely separated, indistinct frontal lamina and subequal pleopods, where pleopods 4–5 are ovate in shape (see also Iverson 1982). There are 17–24 species in this family from central California to Oregon (Brusca et al. 2007). These species belong to the following genera: *Ancinus*, *Clianella*, *Dynamene*, *Paradella*, *Pseudosphaeroma*, *Tecticeps* (all with one species), *Paracereis*, *Sphaeroma* (each with two species), *Dynamenella*, *Exosphaeroma* (each with 4–5 species) (for detailed key of *Exosphaeroma* see Wall et al. 2015) and *Gnorimosphaeroma* has two to four species locally.

The fourth and fifth pleopods in *Gnorimosphaeroma* lack pleats (see Cassidinidae, Fig. 2, Iverson 1982; Fig. 1, Harrison and Ellis 1991), the first pereopod is ambulatory and the uropod is with an exopod. In *G. noblei* the first article of the

left and right antennae peduncles are touching while they are not in *G. oregonense*. *Gnorimosphaeroma rayi*, so far found only in Tomales Bay, California and in Japan, is an estuarine species found also above the mid-tide line, and also under stones. In this species, the basis of the first pereopod has a tuft of 7–9 setae and 2–3 setae are present on the sternal crest of the ischium. *Gnorimosphaeroma oregonense*, is found above the mid-tide line, usually under stones. *Gnorimosphaeroma oregonense* is stouter than *G. insulare*, being 1.5 to 1.75 times longer than wide and all three pleonites reach the lateral margin and the frontal border of its head has several curves (compare Plate 243C to 252C1, Brusca et al. 2007). The exopod of the uropod is only $\frac{2}{3}$ as long as the endopod (Richardson 1905). *Gnorimosphaeroma rayi* also has three pleonites reaching the lateral margin (Fig. 4b) and the basis of the first pereopod is setose. It is stout like *G. oregonense*, and has longer antennae than either *G. oregonense* or *G. insulare*.

Ecological Information

Range: Type locality is San Nicolas Island, California (Menziez 1954). Known range from Alaska to California (Menziez 1954a), where it is most common north of Point Conception (Miller 1968).

Local Distribution: Oregon distribution in the Siuslaw estuary and Cox Island as well as the Metcalf Preserve (South Slough of Coos Bay) and Carter Lake (Wones and Larson 1991).

Habitat: Estuarine intertidal, among *Fucus* and under logs in *Salicornia* marshes and in mud or drainage channels (e.g. Metcalf Preserve) as well as sedge marshes, amongst wood debris and within algal beds and banks (Stanhope et al. 1987). Benthic in Tomales Bay.

Salinity: Euryhaline (Wones and Larson 1991). Estuarine to fresh water and can tolerate salinities from 6–35 (Welton and Miller 1980).

Temperature:

Tidal Level: -1.4 meters to subtidal (Metcalf Preserve, Hoestlandt 1969a).

Associates: Alga *Fucus*, amphipod *Orchestia*, littorine snail *Ovatella* (Metcalf Preserve) and amphipod *Anisogammarus* (Siuslaw estuary). Co-occurs, but is not

negatively affected by the non-native mud snail, *Potamopyrgus antipodarum* (Brenneis et al. 2010).

Abundance: Individuals have a tendency to congregate. Individuals were abundant at some depth in the coastal dune lake, Carter Lake (Oregon National Dunes Recreational Area, Wones and Larson 1991).

Life-History Information

Reproduction: Most isopods have separate sexes (i.e. dioecious, Brusca and Iverson 1985), although protogynous and protandric species are known (Brook et al. 1994; Araujo et al. 2004; Boyko and Wolff 2014). Protogyny has been observed in both *G. insulare* (as *G. luteum*) *G. oregonense*, where females have rudimentary penes and grow to sexually mature males following several molts after brood release (see Table 1, Brook et al. 1994). Reproduction proceeds by copulation and internal fertilization where eggs are deposited within a few hours after copulation and brooded within the female marsupium (Brusca and Iverson 1985). The biphasic molting of isopods allows for copulation; the posterior portion of the body molts and individuals mate, then the anterior portion, which holds the brood pouch, molts (Sadro 2001). Embryonic development proceeds within the brood chamber and is direct with individuals hatching as manca larvae that resemble small adults, with no larval stage (Boyko and Wolff 2014). Little about the reproductive and developmental biology of *G. insulare* is known, but ovigerous females were observed in March, larger females produce larger brood, egg sizes vary from 450–480 µm, and the average developmental time is 120 days (Squamish estuary, British Columbia Canada, Stanhope et al. 1987). *Gnorimosphaeroma rayi* reproduces in spring only, on a one year cycle and *G. oregonensis* has young in spring and fall (Hoestlandt 1969).

Larva: Since most isopods are direct developing, they lack a definite larval stage. Instead this young developmental stage resembles small adults (e.g. Fig. 40.1, Boyko and Wolff 2014). Most isopods develop from embryo to a manca larva, consisting of three stages. Manca larvae are recognizable by lacking the seventh pair of pereopods, but otherwise resemble small adults. They

usually hatch from the female marsupium at the second stage and the molt from second to third manca produces the seventh pair of pereopods and sexual characteristics (Boyko and Wolff 2014). Isopod development and larval morphology can vary between groups (e.g. Gnathiidae, Cryptoniscoidea, Bopyroidae, Cymothoidae, Oniscoidea) (see Boyko and Wolff 2014). Parasitic isopods, for example, have larvae that are morphologically dissimilar from adults (Sadro 2001). Isopod larvae are not common members of the plankton, with parasitic larvae most likely to be observed. Occasionally, suspended benthic juveniles or pelagic species are collected in plankton samples, but these can be differentiated from larvae by their larger size (Sadro 2001). The release of manca larvae in *G. insulare* occurred in July (Stanhope et al. 1987).

Juvenile:

Longevity: The longevity of the congeners *G. rayi* and *G. oregonense* are one year and 2.3 years, respectively (Hoestlandt 1969). An annual, semelparous species, *Gnorimosphaeroma insulare* males die after mating and females die shortly after larvae hatch (Stanhope et al. 1987).

Growth Rate: Growth among isopods occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007), however, isopods do not autotomize limbs as readily as other groups (Brusca and Iverson 1985). Compared to other arthropods, isopods exhibit a unique biphasic molting, in which the posterior 1/2 of the body molts before the anterior 1/2 (Brusca et al. 2007). Growth rates in *G. insulare* were faster in males than females (see Fig. 5, Stanhope et al. 1987).

Food: A detritivore and scavenger. The congener, *G. oregonense*, co-occurs with and readily eats egg capsules of the gastropod *Nucella emarginata*. In fact, predation by this isopod may cause *N. emarginata* to produce egg capsules with thicker walls that are more resistant to predation (Rawlings 1994).

Predators: Isopods play a significant role as intermediate food web links, like amphipods, (e.g. see *Americorophium salmonis*, this

guide) that are consumed by more than 20 species of marine fish (Welton and Miller 1980; juvenile salmonids, sculpins, flounder and rockfish, Stanhope et al. 1987; cabezon, Best and Stachowicz 2012) and whales (Brusca et al. 2007). The presence of the non-native mud snail, *Potamopyrgus antipodarum*, increases predation on *G. insulare* as well as the native isopod *Americorophium salmonis* (Brenneis et al. 2011).

Behavior:

Bibliography

1. ARAUJO, P. B., A. F. QUADROS, M. M. AUGUSTO, and G. BOND-BUCKUP. 2004. Postmarsupial development of *Atlantoscia floridana* (van Name, 1940) (Crustacea, Isopoda, Oniscidea): sexual differentiation and size at onset of sexual maturity. *Invertebrate Reproduction and Development*. 45:221-230.
2. BEST, R. J., and J. J. STACHOWICZ. 2012. Trophic cascades in seagrass meadows depend on mesograzers: variation in feeding rates, predation susceptibility, and abundance. *Marine Ecology Progress Series*. 456:29-42.
3. BOYKO, C. B., and C. WOLFF. 2014. Isopoda and Tanaidacea, p. 210-215. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
4. BRANDT, A., and G. C. B. POORE. 2003. Higher classification of the flabelliferan and related isopoda based on a reappraisal of relationships. *Invertebrate Systematics*. 17:893-923.
5. BRENNIS, V. E. F., A. SIH, and C. E. DE RIVERA. 2010. Coexistence in the intertidal: interactions between the nonindigenous New Zealand mud snail *Potamopyrgus antipodarum* and the native estuarine isopod *Gnorimosphaeroma insulare*. *Oikos*. 119:1755-1764.
6. —. 2011. Integration of an invasive consumer into an estuarine food web: direct and indirect effects of the New Zealand mud snail. *Oecologia*. 167:169-179.
7. BROOK, H. J., T. A. RAWLINGS, and R. W. DAVIES. 1994. Protogynous sex change in the intertidal isopod *Gnorimosphaeroma oregonense* (Crustacea, Isopoda). *Biological Bulletin*. 187:99-111.
8. BRUSCA, R. C., C. R. COELHO, and S. TAITI. 2007. Isopoda, p. 503-541. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
9. BRUSCA, R. C., and E. W. IVERSON. 1985. A guide to the marine isopod crustacea of Pacific Costa Rica. *Revista de Biología Tropical*. 33:1-77.
10. HARRISON, K., and J. P. ELLIS. 1991. The genera of the Sphaeromatidae (Crustacea: Isopoda): A key and distribution list. *Invertebrate Taxonomy*. 5:915-952.
11. HOESTLANDT, H. 1969. Characteristics morphologiques d'une espece nouvelle de la cote pacifique americaine (*G. lutea*). *Comptes Rendus Hebdomadaires des Seances. Academie des Sciences*. 267:1600-1601.
12. —. 1977. Description complementaire de Isopode flabellifere *Gnormosphaeroma insulare* Van Name et synonymie de *G. luteum* Menzies avec cette espece. *Crustaceana*. 32:45-54.
13. IVERSON, E. W. 1982. Revision of the isopod family Sphaeromatidae (Crustacea, Isopoda, Flabellifera) 1. Subfamily names with diagnoses and key. *Journal of Crustacean Biology*. 2:248-254.
14. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
15. MENZIES, R. J. 1954. A review of the systematics and ecology of the genus "Exosphaeroma" with the description of a new genus, a new species, and a new subspecies (Crustacea, Isopoda,

- Sphaeromidae). American Museum of Novitates. 1683:1-23.
16. MILLER, M. A. 1968. Isopoda and Tanaidacea from buoys in coastal waters of the continental United States, Hawaii, and the Bahamas (Crustacea). Proceedings of the United States National Museum. 125:1-53.
 17. —. 1975. Phylum Arthropoda: Crustacea, Tanaidacea and Isopoda, p. 277-312. *In: Light's manual: intertidal invertebrates of the central California coast.* S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
 18. RAWLINGS, T. A. 1994. Encapsulation of eggs by marine gastropods: effect of variation in capsule form on the vulnerability of embryos to predation. *Evolution.* 48:1301-1313.
 19. RICHARDSON, H. 1905. Monograph on the isopods of North America. Bulletin of the United States Natural Museum. 54:727.
 20. RIEGEL, J. A. 1959. A revision in the sphaeromid genus *Gnorimosphaeroma* Menzies (Crustacea: Isopoda) on the basis of morphological, physiological and ecological studies on two of its "subspecies". *Biological Bulletin.* 117:154-162.
 21. SADRO, S. 2001. Arthropoda: Decapoda, p. 176-178. *In: Identification guide to larval marine invertebrates of the Pacific Northwest.* A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 22. STANHOPE, M. J., D. W. POWELL, and E. B. HARTWICK. 1987. Population characteristics of the estuarine isopod *Gnorimosphaeroma insulare* in 3 contrasting habitats: sedge marsh, algal bed, and wood debris. *Canadian Journal of Zoology.* 65:2097-2104.
 23. WALL, A. R., N. L. BRUCE, and R. WETZER. 2015. Status of *Exosphaeroma amplicauda* (Stimpson, 1857), *E. aphrodita* (Boone, 1923) and description of three new species (Crustacea, Isopoda, Sphaeromatidae) from the north-eastern Pacific. *Zookeys:*11-58.
 24. WELTON, L. L., and M. A. MILLER. 1980. Isopoda and Tanaidacea: The Isopods and allies, p. 536-558. *In: Intertidal invertebrates of California.* R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 25. WONES, A. G., and G. L. LARSON. 1991. The benthic macroinvertebrate community in a coastal sand dune lake relative to habitat and changing lake levels. *Hydrobiologia.* 213:167-181.

Updated 2015

Archaeomysis grebnitzkii

A mysid or opossum shrimp

Phylum: Arthropoda
Subphylum: Crustacea
Class: Malacostraca
Order: Mysida
Family: Mysidae

Taxonomy: *Archaeomysis grebnitzkii* was described from a specimen collected from cod gut contents by Czerniavksy in 1882. Later, Holmes described the same species under a different name, *Callomysis maculata*, which was collected from a sandy beach (Holmquist 1975). In 1932, Tattersall transferred *C. maculata* to *A. maculata* and Holmquist (1975) synonymized *Archaeomysis maculata* and *Callomysis maculata* as *A. grebnitzkii*, a species which exhibited a wide North Pacific range (Hanamura 1997; Moldin 2007). These species were previously differentiated by subtle variation in morphological characters that were deemed to be intraspecific (e.g. rostrum shape, third pleopod exopod segments, telson length, Hanamura 1997).

Description

Size: Male body length ranges from 9–15 mm, and females 13–22 mm (Holmquist 1975; Hanamura 1997). The illustrated specimens (from Columbia River) are 4.5 mm (male, Fig. 1a) and 17 mm (female, Fig. 1).

Color: Transparent, with stellar melanophores (“maculate”) (see Fig. 265, Kozloff 1993). Some mysids can change color to blend with their background (Tattersall and Tattersall 1951).

General Morphology: Mysids are shrimp-like crustaceans that are occasionally called opossum shrimp due to the female marsupium or brood pouch, which is composed of oostegites. Like other Peracarida (e.g. cumaceans, isopods, amphipods, tanaids), their bodies are elongated and composed of an anterior **cephalon** and **pereon** (thorax, covered by a **carapace**), and a **pleon** (abdomen). At the posterior end, they have a **telson** and **uropods**. Among the Mysidacea specifically, the carapace is attached to the thorax by anterior segments only and the posterior dorsal edge is free (Banner 1948) (Fig. 1). Mysid eyes are stalked, antennules are biramous, antennae have a long scale (or squama), pleopods are often reduced,

thoracic legs bear swimming exopodites and uropods are lamellar and form tail fan. Mysids are easily distinguished from other Peracardia by the presence of a statocyst on the uropod endopods (see Plate 220, Moldin 2007; Vicente et al. 2014; Fig. 1, Meland et al. 2015).

Cephalon: (see also Figs. 3–4, Hanamura 1997).

Carapace: Attached to first two or three thoracic segments and free dorsally at posterior edge (Banner 1948) (Figs. 1, 1a). Posterior margin with rounded lateral lobes (*Archaeomysis*, Banner 1948) and no fringe or ornamentation. Carapace pronounced anteriorly into a short rostrum (Fig. 2).

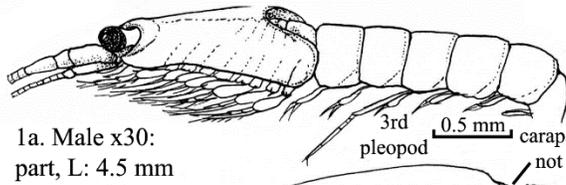
Rostrum: Rostrum length shorter than eyestalk (Fig. 2) and can be grooved, bent down slightly, or rounded (Holmquist 1975). “Shortly produced”, according to original genus description (*Archaeomysis*, Holmquist 1975).

Eyes: Large, movable, stalked, with black corneas and somewhat pear shaped. Eye and eyestalk less than twice as long as broad (Fig. 2). Visual pigment absorbances were measured for *A. grebnitzkii* at 496 nm, which phylogenetically placed this species within a shorter-wavelength spectral sensitivities species clade (Porter et al. 2007).

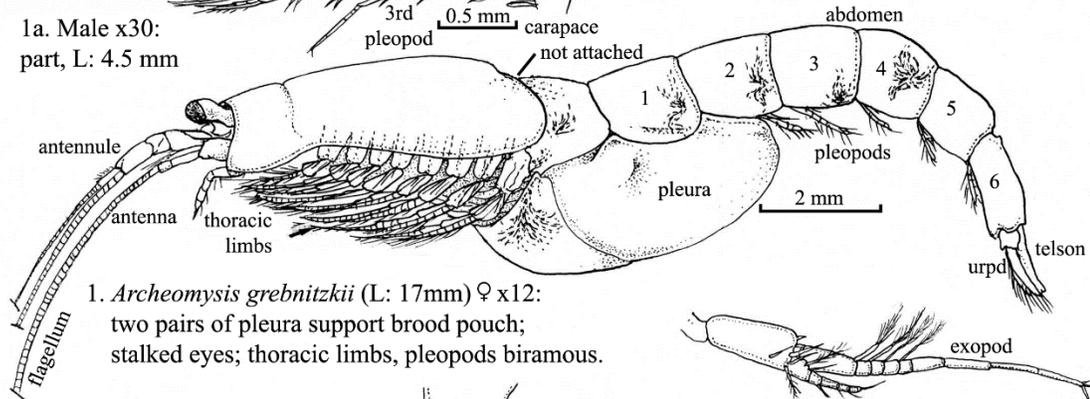
Antennae: Almost as long as body and with slender multi-articulate flagellum (Fig. 1). The peduncle has three joints and is longer than its antennal scale, but shorter than the antennular peduncle (Fig. 2). Antennule peduncle with first joint about equal in length to remaining joints combined. The second joint is with two spines on the outer margin (Tattersall 1951) (Fig. 2).

Antennae Scale: (= squama) Extends to distal end of second peduncular joint and is 3½ times as long as broad. Sclae with straight outer margin, without setae (*Archaeomysis*, Banner 1948), with strong terminal spine, and weak or absent distal suture. On anterior and inner margins, scale

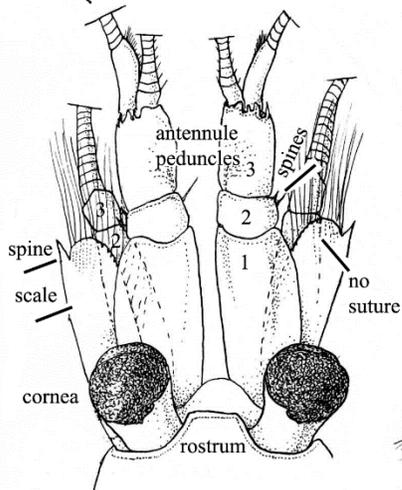
Archeomysis grebnitzkii



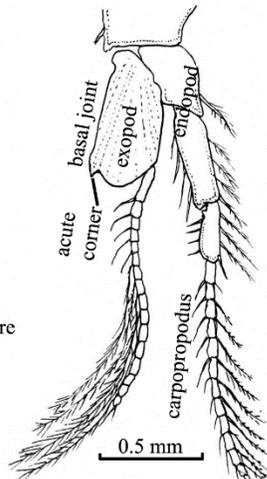
1a. Male x30:
part, L: 4.5 mm



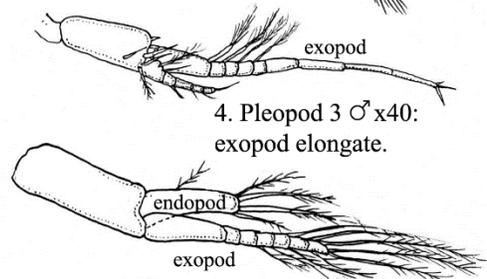
1. *Archeomysis grebnitzkii* (L: 17mm) ♀ x12:
two pairs of pleura support brood pouch;
stalked eyes; thoracic limbs, pleopods biramous.



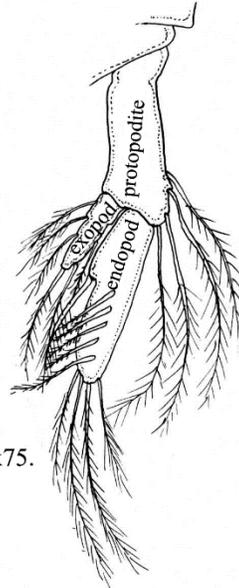
2. Anterior (dorsal view) x40:
rostrum truncate; antennal
scales with strong spine.



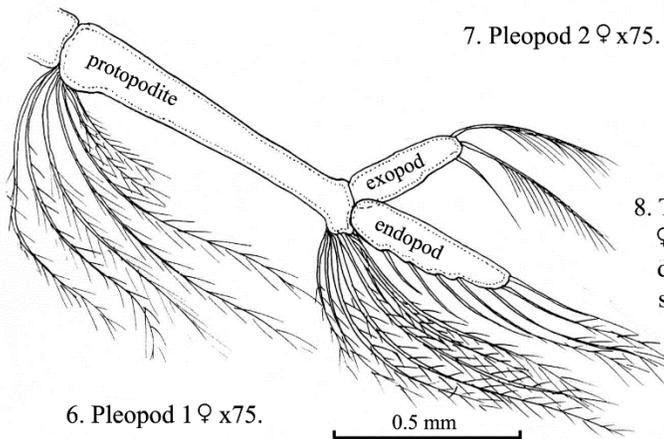
3. 7th thoracic limb ♀ x40.



4. Pleopod 3 ♂ x40:
exopod elongate.



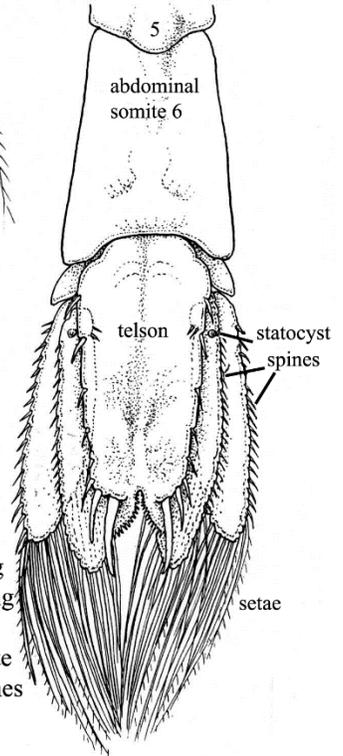
5. Pleopod 4 ♂ x75.



6. Pleopod 1 ♀ x75.

7. Pleopod 2 ♀ x75.

8. Telson and uropods
♀ x40: telson cleft,
denticulate, 8 strong
spines. Uropods: long
endopods with
statocysts; truncate
exopods with spines
on outer margins.



is setose only (no spines) (Kozloff 1974) (Fig. 2).

Mouthparts: For general mouthpart morphology for the Mysida see Fig. 3, Meland et al. 2015. Labrum longer than broad (Tattersall and Tattersall 1951) and with strong frontal spiniform process (*Archaeomysis*, Banner 1948).

Pereon:

Pereopods: Pereopods without well-developed gills (Mysida, Banner 1948). First leg with exopodite, second leg without a lobe-like process on merus. Pereopod 3–8 with carpopropodus (carpus and propodus fused) of endopod that is divided into many subjoints: 9–11 in females (Fig. 3), 7–9 in males (not figured). Exopods in both male and female legs 3–8 has a basal joint with an acute outer distal corner (Fig. 3). No branchiae are present on thoracic legs (Mauchline 1980).

Pleon: Fifth pleonite with a small medial projection and sixth with corresponding ridge (Fig. 5). In females, the lateral pleura on the first somites help form the brood pouch (Fig. 1). Inconspicuous pleura are present on somites 3–5, none on six (Banner 1948).

Pleopods: Male pleopods variable (Mysida, Mauchline 1980) and all are biramous. The first is with a uniarticulate endopod and multi-articulate exopod (Banner 1948) of 7–9 articles (Holmquist 1975) and the third is with elongate exopod (*Archaeomysis*, Banner 1948) (Fig. 1a, 4). The second pleopod with endopod of 4–7 articles, exopod of 8–9 articles, the third is with elongate copulatory exopod of 8–10 articles, endopod of 5 articles (Holmquist 1975) (Fig. 4), and the fourth is with exopod of 5–9 articles (Holmquist 1975). The illustrated fourth male pleopod has 7 articles (Fig. 5), endopod a simple plate, the fifth pleopod is like the fourth, but shorter, and with 4–8 exopod articles (Holmquist 1975) (see also Fig. 4, Hanamura 1997).

Female pleopods are "usually degenerate" (i.e. reduced) (Mysida, Mauchline 1980) and all are biramous (*Archaeomysis*, Mauchline 1980) with each ramus of one small article (see also Fig. 3, Hanamura 1997). The first pleopod is with an elongate protopodite, with basal and distal tufts of long setae, the endopod is longer than the exopod, and more than ½ as long as

protopodite (Fig. 6). The second pleopods are with short protopodite and exopod, and a longer endopod (Fig. 7). The third, fourth and fifth female pleopods are like the second, but with shorter endopods.

Telson: Telson with distinct apical cleft (Mauchline 1980) and margins of cleft are denticulate (Banner 1948) (Fig. 8). Total length is 2½ times as long as broad (at base). Eight to nine spines are present on each margin, the last two spines are long, strong, and close together (Fig. 8) (See Fig. 7, Meland et al. 2015; see Fig. 5, Hanamura 1997).

Uropods: Uropods biramous, with neither branch articulate (Banner 1948). Both rami with setae on the distal margin (*Archaeomysis*, Banner 1948). The endopod is longer than the exopod, with statocyst near base, and two basal spines (Fig. 8). Six spines are present on the inner edge in males, seven in females (Banner 1948). The exopod is truncate, without suture (Mauchline 1980), with 14 (male) to 17 (female) lateral spines on outer margin (more than 10, *Archaeomysis*). No setae on the outer exopod margin (Banner 1948).

Statocyst: Light and balance organ on endopod of uropod (Fig. 8). It is found in all neritic and in common oceanic mysids (Banner 1948) and distinguishes mysids from larval decapods (Green 1968).

Sexual Dimorphism: Pleopod morphology varies between males and females. Mature females are also recognizable by the presence of oostegites that form a thoracic brood pouch with two pairs of lamellae (Mauchline 1980). These oostegites arise from the seventh and eighth pereopods (Mauchline 1980) to form marsupium (Fig. 1).

Possible Misidentifications

Mysidacea and Euphausiacea, being superficially similar in appearance, are often treated together (e.g. Banner 1948; Mauchline 1980). (They were formerly combined as the Schizopoda.) Both are orders of the class Malacostraca, but euphausiids are in the group (i.e. superorder) Eucarida with the Decapoda (Martin 2007). Like the mysids, euphausiids differ from decapods in having biramous thoracic legs (Kasaoka 1974). Unlike the mysids, euphausiids have a carapace that is

fused dorsally with all the thoracic segments. The mysid carapace is attached only to the first two or three thoracic segments. Furthermore, mysid females have oostegites, but euphausiids do not.

Other orders of Peracarida include Isopoda, Tanaidacea, and Amphipoda, which are all fairly easily distinguished from Mysidacea. One order that might be confused is Cumacea, small crustaceans of up to ½ inch long, with an inflated, shrimp-like carapace (see *Cumella vulgaris*, this guide), a single compound recessed eye (except for some eyeless females of some species), and a flexible, tubular abdomen. Mysids characteristically have large, stalked, movable eyes, and well developed exopodites on their thoracic legs. Mature females have oostegites forming a marsupium. Additionally, northeast Pacific mysids lack thoracic gills, have reduced pleopods in females (and sometimes in males). They also have a statocyst on the inner ramus of the uropod.

Mysicadea is divided into two suborders, the Mysida and Lophogastrida. The former suborder comprises coastal and intertidal species while the latter includes mostly large, pelagic and deep sea mysids. These suborders are easily differentiable by the presence of branchial gills, biramous pleopods and the lack of statocysts in Lophogastrida (branchia are absent, pleopods are reduced and statocysts are conspicuous in the Mysida) (Moldin 2007). *Archaeomysis grebnitzkii* belongs to the Mysida, lacking gills or branchiae on the thoracic legs (Fig. 3) and having rather reduced female pleopods.

Within the Mysicadea locally, there are 15 species comprising the following genera: *Acanthomysis* and *Neomysis* (comprising three species and four species, respectively), and *Hyperacanthomysis*, *Alienacanthomysis*, *Columbiaemysis*, *Deltamysis*, *Exacanthomysis*, *Hippacanthomysis*, *Holmesimysis*, and *Archaeomysis* (each with a single species represented locally) (Moldin 2007).

Alienacanthomysis macropsis is recognizable by elongated eyestalks and *Deltamysis holmquistae* has spines on the lateral telson margins, but only distally, where other species have spines all over

the telson margins or in proximal groups. *Alienacanthomysis macropsis*, has a broadly triangular rostrum with long acute lateral carapace spines and its telson has a fringe of small spines. It is abundant in San Francisco Bay and becomes rarer farther north (Holmquist 1979). It has been reported from Yaquina Bay to lower Columbia River and in Puget Sound in bays amongst *Ulva* and in plankton (Kozloff 1974a).

Archaeomysis japonica was described in 1996 by Hanamura et al. and was previously considered *A. grebnitzkii*. However, the two species differ in the endopod of the third pleopod, which is segmented in *A. japonica* (males, Hanamura et al. 1996).

Archaeomysis grebnitzkii has spines along the lateral margins of uropod exopods, which is not seen in other species. Of the species without lateral exopod spines, *Hippacanthomysis platypoda* has a flattened exopod of fourth pleopod (males). *Holmesimysis costata* and *E. davisii* have distinctly segmented pleonites, the former has a broadly triangular telson while the latter has a telson that is sharply triangular. *Holmesimysis* was extracted from *Acanthomysis* (Holmquist 1979). Its members have fourth male pleopods with only two segments and on the tip are two spiny peg-like structures (Mauchline 1980). *Holmesimysis costata*, the type species for the genus, has a short, bluntly rounded antennal scale.

Columbiaemysis, *Acanthomysis*, *Neomysis* and *Hyperacanthomysis* species have pleonites that are smooth and without distinct folds or segments. *Neomysis* species have a pointed distal tip of the antennal scale (see Fig. 3, *Neomysis mercedis*, this guide) and members of the remaining genera have a distal antennal scale tip that is rounded. There are several Pacific species of the genus *Neomysis* (all with pointed apex on the antennal scale, two pairs of female oostegites, statocyst on the uropod endopod, and male fourth pleopods biramous). For differentiating *Neomysis* species, see *N. mercedis* (this guide). *Columbiaemysis ignota* has been described from female specimens only, and only from British Columbia. Its antennal

scale is long, setose all around, and has a suture. Its telson is tongue shaped, with spines becoming dense at the tip, and two long spines at the rounded apex. There are four spines on the lower edge of the statocyst.

Ecological Information

Range: Type locality is Bering and Commander Islands in the Bering Sea (Hanamura 1997). Known range in northern Pacific (Holmquist 1975) from Urup Island and northern Sakhalin to southwest Alaska and the Bering Sea, to Washington, Oregon, and northern California (see Fig. 25, Hanamura 1997).

Local Distribution: Locally present in estuaries of Coos Bay, Yaquina Bay, lower-Columbia River and also along the open coast.

Habitat: Primarily littoral, buried in sand with a mixture of pebbles and boulders on both open ocean coast and in inland waters. In mud and with the alga *Zostera* as well as with *Phyllospadix* and kelp intermixed (Holmquist 1975). Burrows in bottom substratum, and rises to surface of water at night, especially during the breeding season (Mauchline 1980; Tattersall and Tattersall 1951). Individuals very sensitive to oxygen reduction (Green 1968; Jawed 1973).

Salinity: Quite variable, from fresh water to salinities of 34 (Holmquist 1975). However, salinity figures could refer to surface, and the species is an inhabitant of the saltier, bottom water (Holmquist 1975).

Temperature: A wide temperature tolerance, ranging from 8.5 °C or lower to 24 °C. (Holmquist 1975).

Tidal Level: Predominantly intertidal and also found in shallow waters close to shore (Holmquist 1975). Moves up and down with the rising and falling tide. Occurs at extreme low tide level (Puget Sound, Washington, Banner 1948) and subtidal (Coos Bay, Oregon) as well as intertidally and at low water on ocean beaches. Juveniles may be more common higher in the intertidal, while larger individuals (i.e. adults) can be found in deeper habitats, offshore (Llewellyn et al. 1981; Takahashi and Kawaguchi 1995).

Associates:

Abundance: The most common mysid of the northeastern Pacific, followed by *Neomysis*

mercedis (see this guide) (Holmquist 1975). The most abundant and common species collected in hyperbenthic sledge samples at Bastendorff Beach, Charlesteson, Oregon with approximately 3200 individuals per square meter (Marin Jarrin and Shanks 2011).

Life-History Information

Reproduction: All development takes place within the female marsupium and is lecithotrophic and proceeds through three distinct stages: 1) the embryonic stage; 2) the first nauplioid stage (eyeless larva); and 3) the post-nauplioid (eyed larva) stage to a juvenile (see Figs. 38.1–38.2, Vicente et al. 2014). Copulation in *A. grebnitzkii* occurs at night and lasts only a few seconds (Mauchline 1980). Sperm is shed into female brood pouch and the female then lays eggs, which are immediately fertilized (Mauchline 1980) and 510 x 480 µm (a 13 mm long female, Hanamura 1997). Early embryos are spherical or sub-spherical. Young develop to a subadult stage in the brood pouch, and emerge from external genital openings of oviducts near the bases of the sixth thoracic legs (Mauchline 1980). The number of eggs depends on size of female and embryos and in temperate and high latitudes on season, but not on temperature (Mauchline 1980). Brood size in the closely related genus *Gastrosaccus*, can vary seasonally, with largest broods produced in early summer and a female *G. vulgaris*, of similar in size to *A. grebnitzkii* (17 mm long), had 100 embryos per brood (Mauchline 1980). Numbers of broods/year is not definitely known for *A. grebnitzkii*, but the most shallow-living neritic and littoral mysid species usually have three broods year, including the closely related *Gastrosaccus* at a comparable latitude (Japan, Mauchline 1980). Chromosome counts for *A. grebnitzkii* were 2n=10, plus an extra small chromosome (Holmquist 1975). Sex ratios vary within populations, but females frequently outnumber males (Mauchline 1980).

Larva: The first nauplioid stage has appendages that resemble the typical nauplius larva (see *Balanus glandula*, this guide), but lacks an eye or swimming setae. The next post-nauplioid stage has all adult appendages, carapace and eyes. Both stages are non-motile and lecithotrophic.

Ultimately, the post-nauplioid molts into a free-living juvenile (Vicente et al. 2014). Larval development time depends on temperature. In *G. vulgaris*, developmental duration is 10.9–25 days (Matsudaira et al. in Mauchline 1980).

Juvenile: Juveniles are simply miniature adults at post-emergence molt, when they are usually 1.5–3.0 mm long (Mauchline 1980).

Longevity: Mysids will probably live 12–18 months in temperate water and over two years in the Arctic (Tattersall and Tattersall 1951). No longevity rates known for *A. grebnitzkii*. In overwintering generations, most individuals are born in autumn, a few in summer, and fewer in winter. Spring breeding is intensive and females may produce two broods. Spring generations reproduce in the summer (possibly twice), and usually die by autumn (Mauchline 1980).

Growth Rate: Growth among isopods occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007). Mysids generally take about one year to attain full growth and are sexually mature in considerably less time (Tattersall and Tattersall 1951). Females usually grow larger than males (Mauchline 1980) and the number of instars is fewer than for most crustaceans. The first and second occur in the marsupium, and 10 or more occur after the release of young (Mauchline 1980).

Food: Feeds either on living or dead material that is picked up by thoracic endopods, or (more commonly) on fine suspended matter filtered by thoracic exopods. Danish *Gastrosaccus* species, also bottom dwellers, eat detritus, algae, copepods and amphipods (Tattersall and Tattersall 1951). To stir up food for filtering, mysids will balance, head down, on antennal scales and inner flagella of antennulae, and create currents with thoracic exopods. They can also "plow" the bottom with their scales and flagellae (Cannon and Manton 1927 in Mauchline 1980). South African *Gastrosaccus* species feeds most often at night (Mauchline 1980).

Predators: Fish are the most common and most important predators (Tattersall and Tattersall 1951; Haertel and Osterberg 1967)

as well birds (e.g. eider duck in Aleutians), shrimp, ctenophores, squid, and possibly cetaceans and seals. This species is also eaten by humans or used as fish bait in some parts of the world (e.g. India, Tattersall and Tattersall 1951). *Archaeomysis grebnitzkii* was the dominant prey of the bay shrimp, *Lissocrangon stylirostris* (see description in this guide) at night (Marin Jarrin and Shanks 2008, 2011).

Behavior: Locomotion is by exopods of thoracic legs as pleopods are often reduced, and not locomotory. Motion is rotary and unceasing. An "escape mechanism" is also observed in *A. grebnitzkii*, where a sudden downward flex of abdomen and tail fan causes the individual to spring backward and even leap out of water (Tattersall and Tattersall 1951) or through mud (Mauchline 1980). While this has not been shown in *A. grebnitzkii*, females of some mysid species will recapture escaped larvae and return them to their marsupium (Mauchline 1980). Larvae can belong to other individuals or to other species. Males will eat escaped larvae (Mauchline 1980). Mysids avoid bright light (Tattersall and Tattersall 1951), but are attracted to weak light sources and fishing lures (Mauchline 1980). *Archaeomysis grebnitzkii* did not respond to atmospheric pressure changes of 0.1 atm (Mauchline 1980). Other burrowers (e.g. *Gastrosaccus*) have pronounced diel vertical migration where individuals remain within the substrate during the day and are pelagic at night. Burrowing mysids are reotaxtic and face into water current. They may move offshore to avoid breaking waves and waves can also wash them out of their burrows (Mauchline 1980).

Bibliography

1. BANNER, A. H. 1948. A taxonomic study of the Mysidacea and Euphausiacea (Crustacea) of the northeastern Pacific. Part I. Mysidacea, from family Lophogastridae through tribe Erythropini. Transactions of the Royal Canadian Institute. 26.
2. GREEN, J. 1968. The biology of estuarine animals. University of Washington Press, Seattle.

3. HAERTEL, L., and C. OSTERBERG. 1967. Ecology of zooplankton, benthos and fishes in the Columbia River estuary. *Ecology*. 48:459-472.
4. HANAMURA, Y. 1997. Review of the taxonomy and biogeography of shallow-water mysids of the genus *Archaeomysis* (Crustacea: Mysidacea) in the North Pacific Ocean. *Journal of Natural History*. 31:669-711.
5. HANAMURA, Y., S. G. JO, and M. MURANO. 1996. A new species of *Archaeomysis* from coastal waters of Japan (Mysidacea, Gastrosaccinae). *Crustaceana*. 69:553-566.
6. HOLMQUIST, C. 1975. A revision of the species *Archaeomysis grebnitzkii* Czernaivsky (sic) and *A. maculata* (Holmes) (Crustacea, Mysidacea). *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere*. 102:51-71.
7. JAWED, M. 1973. Effects of environmental factors and body size on rates of oxygen consumption in *Archaeomysis grebnitzkii* and *Neomysis awatschensis* (Crustacea, Mysidae). *Marine Biology*. 21:173-179.
8. KASAOKA, L. D. 1974. The male genital system in two species of mysid crustacea. *Journal of Morphology*. 143:259-283.
9. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
10. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
11. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
12. LLEWELLYN, J., D. L. HIGLEY, and R. L. HOLTON. 1981. The life history of the beach dwelling mysid *Archaeomysis grebnitzkii*. *Estuaries*. 4:281-281.
13. MARIN JARRIN, J. R., and A. L. SHANKS. 2008. Ecology of a population of *Lissocrangon stylirostris* (Caridea: Crangonidae), with notes on the occurrence and biology of its parasite, *Argeia pugettensis* (Isopoda: Bopyridae). *Journal of Crustacean Biology*. 28:613-621.
14. —. 2011. Spatio-temporal dynamics of the surf-zone faunal assemblages at a southern Oregon sandy beach. *Marine Ecology*. 32:232-242.
15. MARTIN, J. W. 2007. Arthropoda, p. 411-414. *In: The Light and Smith manual intertidal invertebrates from Central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley.
16. MAUCLINE, J. 1980. The biology of mysids and euphausiids. *Advances in marine biology*. 18:1-681.
17. MELAND, K., J. MEES, M. PORTER, and K. J. WITTMANN. 2015. Taxonomic review of the orders Mysida and Stygiomysida (Crustacea, Peracarida). *Plos One*. 10.
18. MOLDIN, R. F. 2007. Mysidacea, p. 489-495. *In: The Light and Smith manual: intertidal invertebrates from Central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
19. PORTER, M. L., T. W. CRONIN, D. A. MCCLELLAN, and K. A. CRANDALL. 2007. Molecular characterization of crustacean visual pigments and the evolution of pancrustacean opsins. *Molecular Biology and Evolution*. 24:253-268.
20. TAKAHASHI, K., and K. KAWAGUCHI. 1995. Interspecific and intraspecific zonation in three species of sand-burrowing mysids, *Archaeomysis kokuboi*, *A. grebnitzkii*, and *liella ohshimai*, in Otsuchi Bay, northeastern Japan. *Marine Ecology Progress Series*. 116:75-84.
21. TATTERSALL, W. M. 1951. The Mysidacea of the United States National Museum. *Bulletin of the United States National Museum*:1-292.

22. TATTERSALL, W. M., and O. S. TATTERSALL. 1951. The British Mysidacea. Ray Society, London.
23. VICENTE, C. S., G. GUERAO, and J. OLESEN. 2014. Lophogastrida and Mysida, p. 200-205. *In*: Atlas of crustacean larvae. M. J.W., J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.

Updated 2015

Neomysis mercedis

A mysid, or opossum shrimp

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Mysidacea
Family: Mysidae

Taxonomy: *Neomysis awatschensis*, *N. intermedia*, and *N. mercedis* were considered three different species (with distinct morphology) from the western Pacific, northwestern Pacific and northeast Pacific coasts (Tattersall 1951; Holmquist 1973; Brand et al. 1993), but have since been synonymized as *N. mercedis* (Moldin 2007).

Description

Size: Adults range in size from 11 to 17 mm in length (Banner 1948b). The illustrated specimens (from the Columbia River estuary) were up to 17 mm long.

Color: Clear body with black chromatophores, although an individual caught on eelgrass was yellow green (Banner 1948b).

General Morphology: Mysids are shrimp-like crustaceans that are occasionally called opossum shrimp due to the female marsupium or brood pouch, which is composed of oostegites. Like other Peracarida (e.g., cumaceans, isopods, amphipods, tanaids), their bodies are elongated and composed of an anterior **cephalon** and **pereon** (thorax, covered by a **carapace**), and a **pleon** (abdomen). At the posterior end, they have a **telson** and **uropods**. Among the Mysidacea specifically, the carapace is attached to the thorax by anterior segments only and the posterior dorsal edge is free (Banner 1948a) (Fig. 1). Mysid eyes are stalked, antennules are biramous, antennae have a long scale (or squama), pleopods are often reduced, thoracic legs bear swimming exopodites and uropods are lamellar and form tail fan. Mysids are easily distinguished from other Peracardia by the presence of a statocyst on the uropod endopods (see Plate 220, Moldin 2007; Vicente et al. 2014; Fig. 1, Meland et al. 2015).

Cephalon:

Carapace: Not attached dorsally at posterior edge. Anterior lateral angles acute (Figs. 1, 3).

Rostrum: A short triangle with obtusely pointed apex, and rounded, “flanged” corners (Tattersall and Tattersall 1951). A medial depression obscures the pointed apex (Holmquist 1973). In total size, rostrum is only as long as bases of eyestalks (Tattersall and Tattersall 1951) (Figs. 1, 3).

Eyes: On movable stalks and about 1.5 times as long as broad and with corneas that are expanded, but not separated into two portions (Fig. 3).

Antennae: Long, slender, and multi-articulate (Fig. 1).

Antennae Scale: (= squama) Long, narrow, about eight times longer than wide (Banner 1948b; Brandt et al. 1993). The size of the scale, however, may vary among individuals (Holmquist 1973). The scale is setose all around and is with pointed apex pointed (*Neomysis*, Tattersall 1933; Moldin 2007) and an articulated tip (Fig. 3).

Mouthparts: For general mouthpart morphology for the Mysida see Fig. 3, Meland et al. 2015. In *N. mercedis*, the labrum is normal (i.e. not produced posteriorly as a cleft plate, and with anterior sharp point, Tattersall 1933). Anterior is pointed, but not with long sharp spine (Holmquist 1973). The mandibles are without expanded cutting lobe (Banner 1948a).

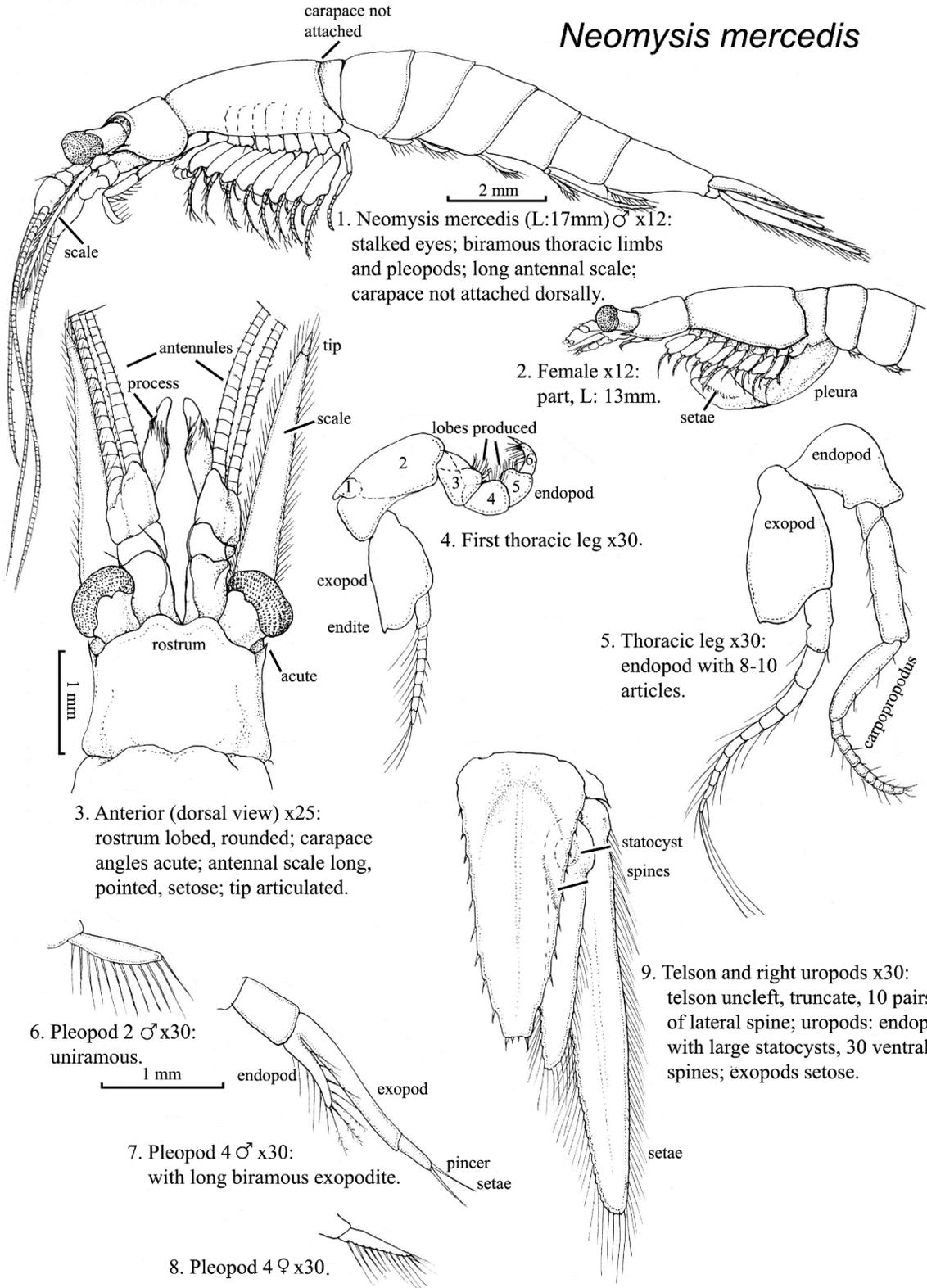
Pereon: Anterior pereonites attached to carapace.

Pereopods: First pereopod with endite of basipodite well developed (Banner 1948b). The endopod has a maxilliped-like feeding structure. The second, third and fourth articles have enlarged lobes (Fig. 4) (Banner 1948b). Legs 3–8 are similar, but third leg is not copulatory (Banner 1948). Endopods with 8–10 articles (Fig. 5).

Pleon:

Pleopods: In males, the first and second pleopods are rudimentary, and the second is uniramous (Banner 1948a) (Fig. 6). The third pleopod is more or less reduced and only the fourth is biramous (*Neomysis*, Banner 1948b). Furthermore, the fourth

Neomysis mercedis



1. *Neomysis mercedis* (L:17mm) ♂ x12: stalked eyes; biramous thoracic limbs and pleopods; long antennal scale; carapace not attached dorsally.

2. Female x12: part, L: 13mm.

4. First thoracic leg x30.

5. Thoracic leg x30: endopod with 8-10 articles.

3. Anterior (dorsal view) x25: rostrum lobed, rounded; carapace angles acute; antennal scale long, pointed, setose; tip articulated.

6. Pleopod 2 ♂ x30: uniramous.

7. Pleopod 4 ♂ x30: with long biramous exopodite.

8. Pleopod 4 ♀ x30.

9. Telson and right uropods x30: telson uncleft, truncate, 10 pairs of lateral spine; uropods: endopods with large statocysts, 30 ventral spines; exopods setose.

pleopod is short and slightly curved in *N. mercedis* (Holmquist 1973; Moldin 2007), with shortened, uniaarticulate endopodite, long exopodite consisting of two articles, and with two terminal pincer setae (Banner 1948b) (Fig. 7). The fifth pleopods are rudimentary. In females, all pleopods are small, uniaarticulate, and rudimentary (Fig. 8).

Telson: Short, and about twice as long as broad. The tip is broadly triangular and not cleft (Brandt et al. 1993). The telson bears 12–15 pairs of lateral spines (Holmquist 1973) (10 in illustrated specimen). The tip has two pairs of spines, the outer pair long and the inner pair very small and not setose (Banner 1948b) (Fig. 9).

Uropods: Uropod endopods with about 30 close set spines along the inner, ventral edge, near the statocyst (Fig. 9). The exopods are undivided, and with setae only (no spines) on both outer and inner margins.

Statocyst: A balance and light organ found on the uropod endopod that is large, opaque, and white in preservation (Fig. 9).

Sexual Dimorphism: The fourth male pleopod is short, slightly curved and biramous. Mature females are recognizable by oostegites and two pairs of lamellae, or pleura. The anterior pair is with posterior "baling lobe" to assist in aerating embryos and has a setose ventral edge (Fig. 2).

Possible Misidentifications

Mysidacea and Euphausiacea, being superficially similar in appearance, are often treated together (e.g. Banner 1948a; Mauchline 1980). (They were formerly combined as the Schizopoda.) Both are orders of the class Malacostraca, but euphausiids are in the group (i.e. superorder) Eucarida with the Decapoda (Martin 2007). Like the mysids, euphausiids differ from decapods in having biramous thoracic legs (Kasaoka 1974). Unlike the mysids, euphausiids have a carapace that is fused dorsally with all the thoracic segments. The mysid carapace is attached only to the first two or three thoracic segments. Furthermore, mysid females have oostegites, but euphausiids do not.

Other orders of Peracarida include Isopoda, Tanaidacea, and Amphipoda, which are all fairly easily distinguished from Mysidacea. One order that might be

confused is Cumacea, small crustaceans of up to ½ inch long, with an inflated, shrimp-like carapace (see *Cumella vulgaris*, this guide), a single compound recessed eye (except for some eyeless females of some species), and a flexible, tubular abdomen. Mysids characteristically have large, stalked, movable eyes, and well developed exopodites on their thoracic legs. Mature females have oostegites forming a marsupium. Additionally, northeast Pacific mysids lack thoracic gills, have reduced pleopods in females (and sometimes in males). They also have a statocyst on the inner ramus of the uropod.

The Mysidacea is divided into two suborders, the Mysida (approximately 1,200 species worldwide) and Lophogastrida (58 species worldwide) (Vicente et al. 2014; Meland et al. 2015). The former suborder comprises coastal and intertidal species while the latter includes mostly large, pelagic and deep-sea mysids. These suborders are easily differentiable by the presence of branchial gills, biramous pleopods and the lack of statocysts in Lophogastrida (branchia are absent, pleopods are reduced and statocysts are conspicuous in the Mysida) (Moldin 2007). *Neomysis mercedis* belongs to the Mysida, lacking gills or branchiae on the thoracic legs and having rather reduced female pleopods.

Within the Mysidacea locally, there are 15 species comprising the following genera: *Acanthomysis* and *Neomysis* (comprising three species and four species, respectively), and *Hyperacanthomysis*, *Alienacanthomysis*, *Columbiaemysis*, *Deltamysis*, *Exacanthomysis*, *Hippacanthomysis*, *Holmesimysis*, and *Archaeomysis* (each with a single species represented locally) (Moldin 2007).

Alienacanthomysis macropsis is recognizable by elongated eyestalks and *Deltamysis holmquistae* has spines on the lateral telson margins, but only distally, where other species have spines all over the telson margins or in proximal groups. *Alienacanthomysis macropsis*, has a broadly triangular rostrum with long acute lateral carapace spines and its telson has a fringe of small spines. It is abundant in San Francisco Bay and becomes rarer farther north (Holmquist 1979). It has been reported from Yaquina Bay to lower Columbia River and in

Puget Sound in bays amongst *Ulva* and in plankton (Kozloff 1974).

Archaeomysis grebnitzkii has spines along the lateral margins of uropod exopods, which is not seen in other species. Of the species without lateral exopod spines, *Hippacanthomysis platypoda* has a flattened exopod of fourth pleopod (males).

Holmesimysis costata and *E. davisii* have distinctly segmented pleonites, the former has a broadly triangular telson while the latter has a telson that is sharply triangular.

Holmesimysis was extracted from *Acanthomysis* (Holmquist 1979). Its members have fourth male pleopods with only two segments and a tip that bears two spiny peg-like structures (Mauchline 1980).

Holmesimysis costata, the type species for the genus, has a short, bluntly rounded antennal scale.

Columbiaemysis, *Acanthomysis*, *Neomysis* and *Hyperacanthomysis* species have pleonites that are smooth and without distinct folds or segments. *Neomysis* species have a pointed distal tip of the antennal scale (Fig. 3) and members of the remaining genera have a distal antennal scale tip that is rounded (Tattersall 1951; Moldin 2007).

Columbiaemysis ignota has been described from female specimens only, and only from British Columbia. Its antennal scale is long, setose all around, and has a suture. Its telson is tongue shaped, with spines becoming dense at the tip, and two long spines at the rounded apex. There are four spines on the lower edge of the statocyst.

There are several northeast Pacific species in the genus *Neomysis* (all with pointed apex on the antennal scale, two pairs of female oostegites, statocyst on the uropod endopod, and male fourth pleopods biramous). *Neomysis japonica* is a Japanese species introduced and first collected from San Francisco Bay, California in 2004. It has a long antennal scale that is 10 times as long as broad, an articulated distal tip, and a broadly triangular telson (Moldin 2007).

Neomysis integer is an Atlantic species that has also been found in plankton in Puget Sound (Kozloff 1974). It has a long pointed antennal scale, a long telson with a narrow, truncate apex and long dense lateral spines, there are about 15 spines near the statocyst. *Neomysis kadiakensis* is a large species (20

to 23 mm long) (Banner 1948b), with over 40 spines near the statocyst. Its telson is long and narrow with 20 or more pairs of lateral spines (Banner 1948b), each spine is longer than the distances between their bases. The eyes have corneas larger than their stalks and the rostrum is bluntly triangular.

Neomysis kadiakensis ranges from British Columbia, Canada to San Francisco Bay, California. Although considered a neritic species, it is possibly more common inside bays and inlets than outside (Banner 1948b). *Neomysis rayii* (= *franciscorum*, = *toion*) has a telson at least 2 ½ times longer than wide and the truncate telson tip is very narrow. There are 10 to 12 pairs of lateral telson spines present and, near the statocyst, are 20 to 50 spines. This is a large species (18 to 65 mm long, Banner 1948b). It ranges from Alaska to San Francisco Bay and occurs in the plankton in Puget Sound, Washington (Kozloff 1974) and has also been collected in Yaquina Bay and the lower Columbia River, Oregon. *Neomysis awatschensis* and *N. intermedia* have been synonymized with *N. mercedis* (Moldin 2007). None of the preceding aforementioned *Neomysis* species, has the short, curved male pleopod with its proximal article 4x the length of its distal article. Also distinctive in *N. mercedis* is the antennal scale, which is 8x longer than wide (Banner 1948b; Brandt et al. 1993).

Ecological Information

Range: Type locality and namesake presumably Lake Merced, California (Holmes 1897 in Tattersall 1951). Known range from Prince William Sound, southern Alaska, to San Francisco Bay area and possibly south to Pt. Conception, California (Orsi and Knutson 1979). Washington in Puget Sound and inland lakes. Oregon sites include Fletcher Lake, rivers and coastal waters and California sites at Lake Merced, Lake Merritt, and the Sacramento-San Joaquin estuary (Holmquist 1973).

Local Distribution: Oregon coastal waters including lagoons, inlets, estuaries, and bays (Holmquist 1973). Planktonic in fresh water, but originated in shallow marine bays, from which it has also moved into fresh water lakes (Banner 1948b). Very sensitive to oxygen content and does poorly in water that has less than 8 ppm (Heuback 1969).

Habitat: Benthic and planktonic in brackish water and freshwater. Rarely found in strictly marine habitats except river mouths. Turbid to clear water (Orsi 1978).

Salinity: Euryhaline, and tolerates a wide range of salinities, but becomes stressed with sudden changes to fresh water (Heuback 1969). Although most members of the Mysidacea are marine, *N. mercedis* has adapted to an estuarine environment, and sometimes occurs in freshwater (e.g. San Joaquin Estuary, Moldin 2007). Especially common in shallow bays with salinities of 10 and less (Banner 1948b). Ranges farther upstream into fresh water than any other *Neomysis* from salinity of 30 (potentially as high as 32.3, Orsi 1978) to entirely fresh water. This species is a model estuarine species for toxicity testing and has been reared at salinities as low as 2 at 17°C on a diet of *Artemia salina* (see Brandt et al. 1993).

Temperature: Eurythermic and tolerates temperature ranges from 7–27 °C in summer, but winter temperature range is unknown (Holmquist 1973). Upper lethal temperature is 25.5 degrees. Population densities are low when temperatures are over 22 degrees, especially when combined with low dissolved oxygen (Heuback 1969).

Tidal Level: Subtidal, but closer to the surface at flood than at ebb tide (Heuback 1969). Depth distribution is highly variable (e.g. eight to more than 30 meter depths in Lake Washington, Chigbu et al. 1998) but individuals tended to be more abundant at shallower stations, with some diel vertical migration observed (deep water during the day, surface water at night, Cooper et al. 1992; Haskell and Stanford 2006). Juveniles do not always exhibit the diel pattern of adults and may be present in surface waters during the day than mature individuals (Siegfried et al. 1979, but see Heuback 1969).

Associates: Sometimes co-occurs with *Archaeomysis grebnitzkii*, but more rarely with *Exacanthomysis davisii*, *Alienacanthomysis macropsis* and other mysids (Holmquist 1982). In the Columbia River Estuary, *A. macropsis* and *N. mercedis* females host generally inconspicuous ectoparasitic copepods (*Hansenulus trebax*) within their marsupium (see Fig. 2, Daly and Damkaer 1986). Thirty-six percent of brooding females were infected with these copepods, which

feed on developing embryos within the marsupium (Columbia River Estuary, Oregon, Daly and Damkaer 1986).

Abundance: Second most common mysid of the northeastern Pacific after *A. grebnitzkii* (Holmquist 1982). In Coos Bay, Oregon, densities varied from zero to 29 individuals per cubic meter (summer, Ziegler 1983). Abundance peaks were observed on May 26, July 3 (highest) and July 24 and correlated with high temperatures, chlorophyll counts, and possibly reproductive swarming. In the California Delta, densities drop off when temperatures are over 18°C, light intensity is high, salinities less than 10 and when little flow reversal occurs at flood tide. Low population densities were observed in Lake Washington and ranged from 0.1–0.17 mysids per cubic meter in 1991 and 1992 (Chigbu 2004).

Life-History Information

Reproduction: All mysid development takes place within the female marsupium, is lecithotrophic and proceeds through three distinct stages: 1) the embryonic stage; 2) the first nauplioid stage (eyeless larva); and 3) the post-nauplioid (eyed larva) stage to a juvenile (see Figs. 38.1–38.2, Vicente et al. 2014). *Neomysis mercedis* individuals are reproductive during most of year, but few gravid females are observed in December and January (Heuback 1969) and peak reproductive time is in summer months. Brood size depends on female body size, egg size, and season (in high and temperate latitudes) (Johnston and Northcote 1989). Estuarine *N. mercedis* females 7–17 mm long had 5–57 eggs per brood (Heuback 1969; Cooper et al. 1992). The percentage of small gravid females (7–10 mm) was greatest late summer and fall with most mortality occurring thereafter; remaining females lacked marsupium in winter. Females 11–12 mm long were gravid most of year, and produced the most eggs in early summer months. Large females (over 13 mm), were gravid in late winter and spring (California Delta, Heuback 1969). Females may produce 1–5 broods per year (Daly and Damkaer 1986; Johnston and Northcote 1989). Coos Bay brood time is probably 5 weeks (Ziegler 1983).

Larva: The first nauplioid stage has appendages that resemble the typical nauplius larva (e.g. see *Balanus glandula*, this guide), but lacks an eye or swimming setae. The next post-nauplioid stage has all adult appendages, carapace and eyes. Both stages are non-motile and lecithotrophic. Ultimately, the post-nauplioid molts into a free-living juvenile (Vicente et al. 2014). Newly hatched individuals are approximately 1 mm in cephalothorax length (Figs. 1–2, Brandt et al. 1993).

Juvenile: Juvenile *N. mercedis* range in size from 1–3 mm in length (Siegfried et al. 1979; Brandt et al. 1993).

Longevity: *Neomysis integer* lifespan is probably 12 to 18 months, but lives are shorter in dense cultures of diatoms and diatom-free water (see Lucas in Tattersall and Tattersall, 1951) or in the lab (e.g. 150 days, Brandt et al. 1993).

Growth Rate: Growth among mysids occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autotomized (Kuris et al. 2007). In Japanese *Neomysis*, the May generation matured in 1 ½ months and the August generation matured the following April (Tattersall and Tattersall 1951). After hatching, individuals are 1 mm (cephalothorax length) and grow to 3.5 mm after 60 days (see Fig. 1, Brandt et al. 1993). Size at sexual maturity ranged from 9–20 mm in two Canadian lakes (Kennedy and Muriel Lakes, respectively, Cooper et al. 1992).

Food: Mysids are generally omnivorous and eat detritus, algae and zooplankton by filtration (Siegfried and Kopache 1980; Moldin 2007). Individuals preferred large diatoms in the California Delta, but 80% of energy came from rotifers and copepods (Kost and Knight 1975; Siegfried and Kopache 1980).

Neomysis mercedis is not an active predator and captures prey in a self-generated current. Adults feed continuously, especially at night and juveniles eat rotifers when available, but not copepods. Individuals will eat *Artemia salina* nauplii in the lab (Siegfried and Kopache 1980; Brandt et al. 1993). In the Fraser River, British Columbia, *N. mercedis* eats harpacticoid copepods (Johnston and

Lasenby 1982) and in Lake Washington, the cladoceran *Daphnia* (Murtaugh 1981a, 1981b; Chigbu and Sibley 1994; Chigbu 2004). In the lab, *N. integer* consumed on average of over 1 million cells, and maximum of 6 million cells, of the diatom, *Nitzschia*, per hour (See Lucas in Tattersall and Tattersall 1951).

Although *N. mercedis* is also a food source for juvenile salmonids and other fishes (see **predators** below), this mysid is also a competitor that consumes the same zooplankton prey as several common pelagic fish (e.g. sockeye salmon, Cooper et al. 1992; Hyatt et al. 2005; American shad and chinook salmon, Haskell and Stanford 2006).

Predators: A primary food for fishes of upper bays and the principal food source of young of the year striped bass in the California Delta (Murtagh 1981a). Also eaten by American shad, white sturgeon, white catfish, caridean shrimp and juvenile Chinook salmon (Tiffan et al. 2014) and striped bass (Siegfried and Kopache 1980). Longfin smelt may regulate the abundance of *N. mercedis*, according to a study from Lake Washington from 1988 to 1992 (Chigbu and Sibley 1998; Chigbu et al. 1998). Additional predators include the carnivorous shrimp, *Crangon franciscorum* and *Palaemon macrodactylus* (Sacramento-San Joaquin River Delta, California, Siegfried 1982).

Behavior: In sea water, individuals tend to avoid light when in dense diatom cultures (Tattersall and Tattersall 1951).

Bibliography

1. BANNER, A. H. 1948a. A taxonomic study of the Mysidacea and Euphausiacea (Crustacea) of the northeastern Pacific. Part I. Mysidacea, from family Lophogastridae through tribe Erythropini. Transactions of the Royal Canadian Institute. 26.
2. ——. 1948b. A taxonomic study of the Mysidacea and Euphausiacea (Crustacea) of the Northeastern Pacific. Part II: Mysidacea from tribe Mysini through subfamily Mysedellinae. Transactions of the Royal Canadian Institute. 27:65-125.
3. HAIR, J. R. 1971. Upper lethal temperature and thermal shock tolerances of the opossum shrimp, *Neomysis awatschensis*, from the Sacramento-San Joaquin Estuary, California. California Fish

- and Game. 57:17-27.
4. HEUBACH, W. 1969. *Neomysis awatschensis* in the Sacramento-San Joaquin River estuary. *Limnology and Oceanography*. 14:533-546.
 5. HOLMQUIST, C. 1973. Taxonomy, distribution and ecology of the three species *Neomysis intermedia* (Czerniavsky), *N. awatschensis* (Brandt) and *N. mercedis* Holmes (Crustacea, Mysidacea). *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere*. 100:197-222.
 6. ———. 1981. The genus *Acanthomysis* Czerniavsky, 1882 (Crustacea:Mysidacea). *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere*. 108:386-415.
 7. ———. 1979. *Mysis costata* Holmes, 1900, and its relations (Crustacea, Mysidacea). *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere*. 106:471-499.
 8. ———. 1982. Mysidacea (Crustacea) secured during investigations along the west coast of North America by the National Museums of Canada, 1955-1966, and some inferences drawn from the results. *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere*. 109:469-510.
 9. JOHNSTON, N. T., and D. C. LASENBY. 1982. Diet and feeding of *Neomysis mercedis* Holmes (Crustacea, Mysidacea) from the Fraser River Estuary, British Columbia. *Canadian Journal of Zoology*. 60:813-824.
 10. KOZLOFF, E. N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle & London.
 11. MAUCLINE, J. 1980. The biology of mysids and euphausiids, p. 681. *In: Advances in marine biology*. Vol. 18. J. H. S. Blaxter, F. S. Russell, and C. M. Yonge (eds.). Academic Press, London; New York.
 12. MURTAUGH, P. A. 1981. Selective Predation by *Neomysis mercedis* in Lake Washington. *Limnology and Oceanography*. 26:445-453.
 13. ORSI, J. J., and A. C. KNUTSON. 1979. An extension of the known range of *Neomysis mercedis*, the opossum shrimp. *California Fish and Game*. 65:127-130.
 14. SIEGFRIED, C. A., and M. E. KOPACHE. 1980. Feeding of *Neomysis mercedis* (Holmes). *Biological Bulletin*. 159:193-205.
 15. TATTERSALL, W. M. 1932. Contributions to a knowledge of the Mysidacea of California. I. On a collection of Mysidae from La Jolla, California. University of California Press, Berkeley, Calif.
 16. ———. 1933. Euphausiacea and Mysidacea from Western Canada. *Contributions to Canadian Biology and Fisheries*. 8:181-205.
 17. TATTERSALL, W. M., and O. S. TATTERSALL. 1951. *The British Mysidacea*. Ray Society, London.
 18. TURNER, J. L., and W. HEUBACH. 1966. *Distribution and concentration of Neomysis awatschensis in the Sacramento-San Joaquin Delta*. *California Fish and Game*. 133:105-112.
 19. ZIEGLER, R. 1983. A study of *Neomysis mercedis* in the Coos River., p. 13. University of Oregon Institute of Marine Biology, Charleston, Oregon.

Updated 2015

Leptocheilia sp.

A green tanaid

Phylum: Arthropoda, Crustacea
Class: Malacostraca
Order: Tanaidacea, Tanaidomorpha
Family: Leptocheliidae

Taxonomy: The taxonomic history of *Leptocheilia dubia* and *L. savignyi* is confusing and remains to be resolved. In 1842, Krøyer described *Tanais dubia* and *Tanais savignyi*, the former species possessing one less segment on the uropod endopod. These species were later transferred to the new genus *Leptocheilia* based on their elongate cheliped morphology. Due to morphological disparity between males and females, some *Leptocheilia* females were described as new species, including the genus *Paratanais*. Eventually, most of the variation between individuals (males and females) of newly described species was determined to be intraspecific and species were synonymized under the “*L. dubia* group” (= “*Leptochelieae*-Group 2”, Lang 1973 in Ishimaru 1985), which included *L. savignyi*, among others. This group encompasses a wide geographic distribution (Miller 1968) and it is likely composed of several cryptic species (Cohen 2007; Jarquin-Gonzalez et al. 2015). In 2010, Bamber redescribed *L. savignyi* to include many of the species previously in the “*L. dubia* group”, but the full synonymy of the two species is still uncertain. Because the name *L. savignyi* is older, there is also current debate around which name should be the senior synonym (Cohen 2007; Bamber 2010). Until the taxonomy is resolved we will use the name *Leptocheilia* sp., but for the sake of clarity we include species names used by authors we cite.

Description

Size: Individuals are rather small, up to 1 cm in length. The illustrated specimen (from South Slough of Coos Bay) was 6 mm in length. British Canadian species were reported to 4.5 mm (Fee 1927).

Color: Transparent white to light green with some specimens bearing slight orange tinge (Kozloff 1993; Cohen 2007). Brightly colored females were found in early spring (South Slough of Coos Bay) that had red striped

antennae. Males found in August were almost transparent.

General Morphology: Tanaids resemble small, elongated and dorso-ventrally flattened lobsters with claws that extend anteriorly. Their bodies can be divided into three sections, a cephalothorax (**cephalon** and first two **pereonites**), a thorax or **pereon** (including **pereonites** 3–8) and a **pleon** (abdomen), consisting of **pleonites**, with the posterior-most fused with the telson (**pleotelson**), and five pairs of **pleopods** as well as a single pair of **uropods** (see Plate 253A, Cohen 2007). *Leptocheilia dubia* is a tube dweller (Cohen 2007) and resembles a slender isopod (see Fig. 340, Kozloff 1993).

Cephalon: Head narrows anteriorly and is fused with first two thoracic segments (Tanaidacea) (Fig. 1).

Carapace:

Eyes: Stalked, large, and anterolateral (Figs. 1, 2).

Antenna 1: Male first antenna is long, and has flagellum with seven articles (Fig. 2). The female first antenna, on the other hand, is short, and consists of three articles (Figs. 1, 4).

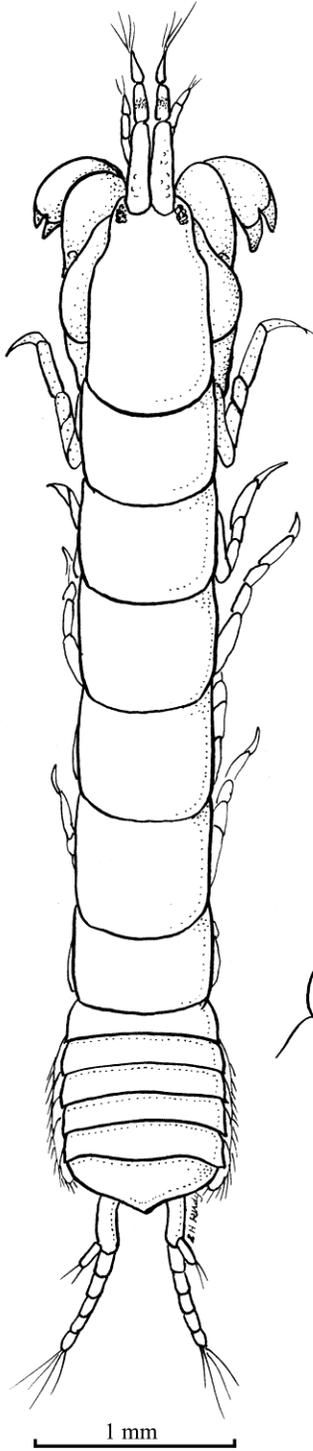
Antenna 2: Male second antenna is shorter than the basal article of the first antennae and consists of four articles (Fig. 2). The female second antenna is longer than that of the male, also with four articles (Fig. 1).

Mouthparts: Fused in males, and can be dissected in females. Mandible is without palp (Tanaidomorpha, Fig. 3).

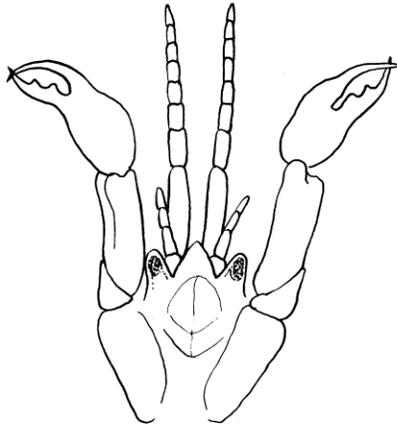
Chelipeds: Chelipeds are very prominent, but sexually dimorphic. Male chelipeds are long and slender and with carpus longer than basal article of the first antenna (Figs. 2, 5). The propodus is shorter than the fingers, which have two teeth on the inner side (Fig. 5). Female chelipeds are short and heavy (Figs. 1, 6).

Pereon: Consists of six uniform segments (Fig. 1).

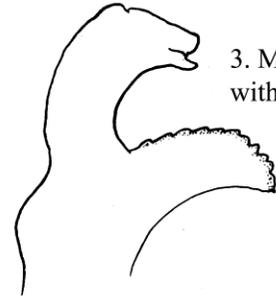
Leptocheilia sp.



1. *Leptocheilia* sp. ♀ x32:
carapace: head, first two segments fused, six thoracic segments, five abdominal segments, and telson.

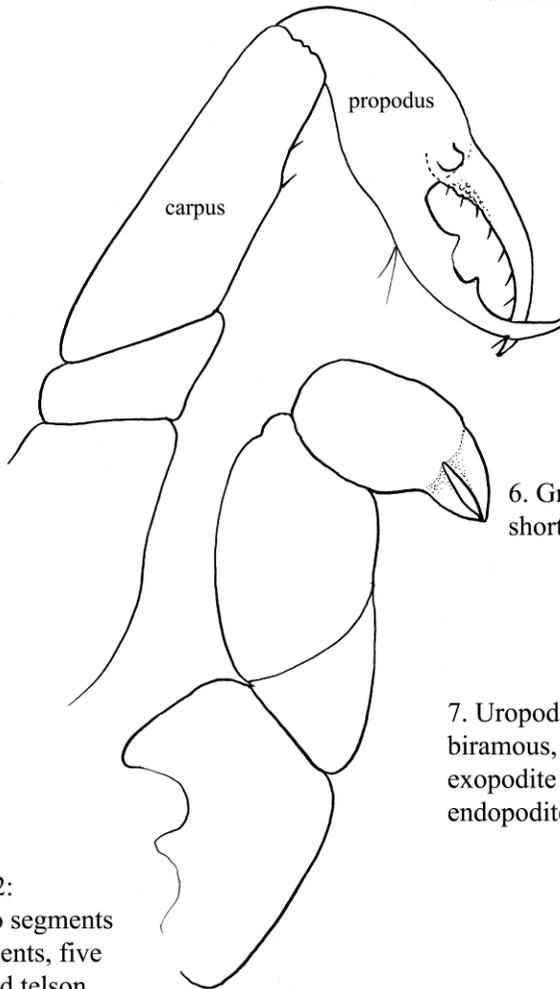
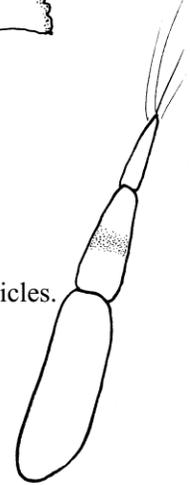


2. Head ♂ (ventral view):
long first antenna, with seven articles in flagellum, eyes separate from head, long chelipeds.



3. Mandible ♀:
without palp.

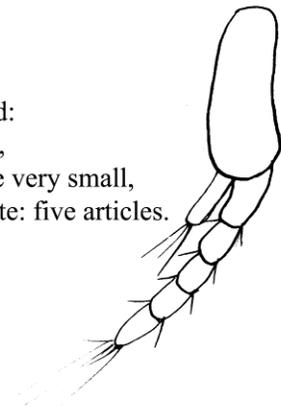
4. First antenna ♀:
uniramous, three articles.



5. Gnathopod ♂ x100:
carpus longer than basal article of first antenna, propodus shorter than fingers, fingers with two teeth.

6. Gnathopod ♀:
short, heavy chela.

7. Uropod:
biramous,
exopodite very small,
endopodite: five articles.



Pereopods: Six pairs plus the anterior chelate gnathopods (see **chelipeds**). A small and inconspicuous penal process is attached between the last pair of these legs in the male.

Pleon: Consists of five similar segments and a telson (Fig. 1).

Pleopods: Five pleopod pairs are biramous and leaf-like.

Uropods: Both sexes have biramous uropods, with exopodite very small and endopodite consisting of five articles (Fig. 7).

Pleotelson: Fused with posterior pleonite and bears medial posterior point (Fig. 1).

Sexual Dimorphism: The first **antenna** is longer in males than females, while the opposite is true for the second antenna.

Chelipeds are long and slender in males (Fig. 5) and short and stout in females (Fig. 6) (Kozloff 1993), a character that lead many taxonomists to describe them as separate species (see **Taxonomy**).

Possible Misidentifications

The Tanaidacea differ from the closely related Isopoda in the number of pereonites generally present: six in tanaids and seven in isopods. In addition, tanaids have a jointed uropod branch and pair of chelipeds anteriorly. The three tanaidacean suborders proposed by Sieg (1980) include Apseudomorpha, Neotanaidomorpha and the Tanaidomorpha, to which *Leptochelia* belongs. Members of the Apseudomorpha and Tanaidomorpha occur locally (Cohen 2007). Apseudomorpha species are not tube dwellers, they have a biramous flagellum of the first antenna, they sometimes lack pleopods, they have mandibles with palps (3-articulated), and the marsupium in females is composed of four pairs of oostegites only. Conversely, the Tanaidomorpha are usually tube-dwellers and are characterized morphologically by an unbranched flagellum of the first antenna, mandibles without palps, the presence of pleopods, and a marsupium consisting of 1–4 pairs of oostegites.

Within the Tanaidomorpha there are at least two local families, the Tanaidae and the Leptocheliidae (see Cohen 2007). The Tanaidae are characterized by 3–5 pleonites plus a pleotelson and three pairs of pleopods,

while Leptocheliidae species have five pleopods.

The genus *Leptochelia* is the only one in the family Leptocheliidae occurring locally, but the number of species is currently unknown. *Leptochelia dubia* is suspected to be a complex of several species and may or may not be synonymized with *L. savignyi* (Cohen 2007) (see **Taxonomy**). *Leptochelia savignyi* from Puget Sound, has four (sometimes six) segments in the endopodite of the uropod (Kozloff 1974), has larger eyes and stubbier first antennae than does *L. dubia* (Lang 1957). In *L. savignyi* the first free thoracic segment is shorter than the others, but they are fairly equal in *L. dubia*. The male chelipeds of the two species are almost identical. For re-description of *L. savignyi*, see Bamber 2010. *Leptochelia filum*, another Puget Sound species is small (2.5 mm), white, and found at 37 meters sandy benthos, which is quite a different habitat from that of *L. dubia*. The endopodite of the uropod in this species has 3–4 articles, and not five as in *L. dubia*.

Ecological Information

Range: Type locality is off Brazil (Bamber 2010). Cosmopolitan (see Miller 1968) and is almost certainly an assemblage of several divergent species (Cohen 2007; Jarquin-Gonzalez et al. 2015). Northwest distribution from Puget Sound, Washington to southern California (Cohen 2007).

Local Distribution: In Coos Bay at Metcalf preserve and South Slough. Also found at Tillamook Bay (Forsberg et al. 1977).

Habitat: A tube-dweller, *L. dubia* is found in flimsy slime tubes much like those of amphipod *Americorophium* (see *A. brevis*, this guide), in a substrate of mud and wood chips (e.g. Metcalf Preserve). Additional habitats include dead coral (Richardson 1902; Lewis 1998), sponge beds (at 45 meters, Fee 1927), within sand in the strand line at low tide (Hatch 1947), and near the water surface on hydroids and algae (Fee 1927). The upper limit of sand grain size is 200 μm (Wieser 1959). Higher abundances of *L. dubia* were observed in areas of intermediate or low pH (see Tables 1–2, Cigliano et al. 2010). *Leptochelia savignyi* was found at the ends of empty spionid polychaete (*Dipolydora armata*) burrows or amongst calcareous hydrozoan

(*Millepora complanata*) branches in Barbados (Lewis 1998). Individuals were reported to be particularly dense, although not necessarily males or reproductive females, on the calcareous green macroalga, *Penicillus capitatus* (Stoner 1986).

Salinity: Collected at salinities of 30.

Temperature:

Tidal Level: +0.9 meters (Metcalf Preserve) to 45 meters (Fee 1927). In Tomales Bay, California, tidal level ranged from +0.5 meters and -0.8 MLLW, with highest density reported at -0.5 MLLW (Mendoza 1982).

Associates: Associates include the amphipod, *Americorophium*, small polychaetes, and the clam, *Macoma nasuta*. *Leptochelia dubia* exhibited a positive response to the presence of mussel mats created by the non-native mussel *Musculista senhousia*, potentially due to the additional structure and substrate the mats provide for tube building (Crooks and Khim 1999).

Abundance: The dominant invertebrate, when observed (e.g., Metcalf Preserve) and can be present in enormous numbers (Kozloff 1993). In False Bay, San Juan Island, Washington, *L. dubia* was an abundant species, with average density 416 to 2,600 individuals per sediment sample (100 square cm by 14 cm deep, Brenchley 1981). Average densities can be very high and were reported to be greater than 30–50,000 individuals per square meter (Tomales Bay, California, Mendoza 1982; Friday Harbor, Washington, Highsmith 1983).

Life-History Information

Reproduction: Tanaidaceans are gonochoristic, sequentially (protogynous) or simultaneously hermaphroditic (Highsmith 1983; Boyko and Wolff 2014) and sexual reversal may be determined by environmental factors (e.g. temperature, Masanuri 1983; Highsmith 1983). Reproduction in tanaidaceans, like isopods, is direct and proceeds within the female brood chamber (i.e. marsupium) to a larval form, called a manca that resembles a small adult. Oviparous *L. dubia* females and nests of young were found in February and in Tomales Bay, California, brooding females were found throughout the year (see Fig. 5, Mendoza 1982). Female size is positively correlated to brood size. Young females occasionally

transition into males before they reach sexual maturity (Kozloff 1993). Fighting occurs among males and larger males tend to win fights and dominate within the population. However, the entire population is usually sex-skewed strongly toward females (Mendoza 1982; Highsmith 1983; Stoner 1986). However, more males were observed, locally, in August at Metcalf Preserve.

Larva: Since most tanaidaceans are direct developing, they lack a definite larval stage. Instead, this developmental stage resembles small adults (e.g. Fig. 40.2, Boyko and Wolff 2014). Most tanaidaceans develop from embryo to a manca larva, comprising of four stages. Larvae hatch from the female marsupium at the second manca stage (the first and second manca stages are not marked by a molt, Boyko and Wolff 2014). The third manca stage in tanaidaceans has partially developed sixth pereopods, and the first and second pereonites are fused with the cephalon as in adults. The fourth manca stage can be recognized by the presence of small pleopods (Boyko and Wolff 2014) (but only in those species that possess pleopods like *L. dubia*). Dispersal by rafting is a possibility for this small species that requires very little sediment and diatoms for food (Highsmith 1985). Manca larval stages in *L. savignyi* were described by Masunari (1983). The manca II stage was 880 μm in length (range 650–1,100 μm), lacked the last pairs of pereopods and pleopods and had uropodal endopods of three segments. Manca III were 1,050 μm in length (range 700–1,400 μm) and possessed all pereopods and pleopods. Masunari (1983) described two post-manca stages called neutrum I and II. In the first, all pereopods and pleopods were fully developed and body length was 1,580 μm , and in the second, uropodal endopods were composed of four segments (rather than three in all previous stages) and mean body length was 4,000 μm (see Fig. 1, Masunari 1983).

Juvenile: Newly released juveniles were 600–700 μm in length (Mendoza 1982) and resemble small adults, with fully formed pereopods and pleopods (Boyko and Wolff 2014).

Longevity:

Growth Rate: Growth among isopods occurs in conjunction with molting where the exoskeleton is shed and replaced. Post-molt

individuals will have soft shells as the cuticle gradually hardens. During a molt, arthropods have the ability to regenerate limbs that were previously autonomized (Kuris et al. 2007).

Food: Detritus and associated micro-organisms, often scraped from the surface of larger organisms (Kozloff 1993).

Predators: Predators of this small tanaidacean include many fishes. For example, *Parophrys vetulus* (English Sole), *Platichthys stellatus* (Starry Flounder), and *Oncorhynchus tshawytscha* (Chinook Salmon) (Tillamook Bay, Forsberg et al 1977), and juvenile *Leptocottus armatus* (Staghorn Sculpin) (Tamales Bay, California, Mendoza 1982). *Leptocheilia dubia* populations showed a larger abundance when the non-native and co-occurring green crab (*Carcinus maenas*) was removed (Bodega Bay, California Grosholz et al. 2000) suggesting predation or competition between the two species.

Behavior: Cements together particles to construct a tube, and in doing so stabilizes the substrate (Kozloff 1993). The rate of tube building is 70–600 (average 350) grams per square meter per day, with highest rates occurring during autumnal months and lowest in late-winter months (Yaquina Bay, Oregon, Krasnow and Taghon 1997). The tube of *L. savignyi* is 400 μm in diameter, 1 cm in length and is open at both ends (Lewis 1998).

Bibliography

1. BAMBER, R. N. 2010. In the footsteps of Henrik Nikolaj Kroyer: the rediscovery and redescription of *Leptocheilia savignyi* (Kroyer, 1842) sensu stricto (Crustacea: Tanaidacea: Leptocheliidae). Proceedings of the Biological Society of Washington. 123:289-311.
2. BOYKO, C. B., and C. WOLFF. 2014. Isopoda and Tanaidacea, p. 210-215. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
3. BRENCHLEY, G. A. 1981. Disturbance and community structure: an experimental study of bioturbation in marine soft-bottom environments. *Journal of Marine Research*. 39:767-790.
4. CIGLIANO, M., M. C. GAMBI, R. RODOLFO-METALPA, F. P. PATTI, and J. M. HALL-SPENCER. 2010. Effects of ocean acidification on invertebrate settlement at volcanic CO₂ vents. *Marine Biology*. 157:2489-2502.
5. COHEN, A. N. 2007. Tanaidacea, p. 542-545. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley.
6. CROOKS, J. A., and H. S. KHIM. 1999. Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *Journal of Experimental Marine Biology and Ecology*. 240:53-75.
7. FEE, A. R. 1927. The Isopoda of Departure Bay and vicinity with descriptions of new species, variations and colour notes. *Contributions to Canadian Biology and Fisheries*. 3:15-47.
8. FORSBERG, B. O., J. A. JOHNSON, and S. I. KLUG. 1977. Identification, distribution and notes on food habits of fish and shellfish in Tillamook Bay, Oregon. Oregon Department of Fish and Wildlife, s.l.
9. GROSHOLZ, E. D., G. M. RUIZ, C. A. DEAN, K. A. SHIRLEY, J. L. MARON, and P. G. CONNORS. 2000. The impacts of a nonindigenous marine predator in a California bay. *Ecology*. 81:1206-1224.
10. HATCH, M. H. 1947. The Chelifera and Isopoda of Washington and adjacent regions. University of Washington Publications in Biology. 10:155-274.
11. HIGHSMITH, R. C. 1983. Sex reversal and fighting behavior: coevolved phenomena in a tanaid crustacean. *Ecology*. 64:719-726.
12. —. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. *Marine Ecology Progress Series*. 25:169-179.
13. ISHIMARU, S. I. 1985. A new species of *Leptocheilia* (Crustacea Tanaidacea) from Japan with a redescription of *Leptocheilia savignyi*.

- Publications of the Seto Marine Biological Laboratory. 30:241-268.
14. JARQUIN-GONZALEZ, J., M. DEL SOCORRO GARCIA-MADRIGAL, and L. FERNANDO CARRERA-PARRA. 2015. First species of *Leptochelia* Dana, 1849 (Crustacea: Tanaidacea) from the Eastern Pacific, with an annotated checklist and identification keys for the genus. *Zootaxa*. 3920:501-533.
 15. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
 16. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle, WA.
 17. KRASNOW, L. D., and G. L. TAGHON. 1997. Rate of tube building and sediment particle size selection during tube construction by the tanaid crustacean, *Leptochelia dubia*. *Estuaries*. 20:534-546.
 18. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 19. LANG, K. F. 1957. Tanaidacea from Canada and Alaska. *Contributions du Departement des Pecheries, Quebec*. 52:1-54.
 20. —. 1973. Taxonomische und phylogenetische Untersuchungen über die Tanaidaceen (Crustacea). *Zoologica Scripta*. 2:197-229.
 21. LEWIS, J. B. 1998. Occurrence and distribution of the tanaid crustacean *Leptochelia savignyi* on the calcareous hydrozoan *Millepora complanata*. *Bulletin of Marine Science*. 63:629-632.
 22. MASUNARI, S. 1983. Postmarsupial development and population dynamics of *Leptochelia savignyi* (Kroyer, 1842) (Tanaidacea). *Crustaceana*. 44:151-162.
 23. MENDOZA, J. A. 1982. Some aspects of the autecology of *Leptochelia dubia* (Kroyer, 1842) (Tanaidacea). *Crustaceana*. 43:225-240.
 24. MILLER, M. A. 1968. Isopoda and Tanaidacea from buoys in coastal waters of the continental United States, Hawaii, and the Bahamas (Crustacea). *Proceedings of the United States National Museum*. 125:1-53.
 25. RICHARDSON, H. 1902. The marine and terrestrial Isopods of the Bermudas, with descriptions of new genera and species, *Leptochelia dubia*. *Transactions of the Connecticut Academy of Sciences*. 11:277-310.
 26. SIEG, J. 1980. Taxonomic monograph on the Tanaids (Crustacea, Tanaidacea). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*. 537:1-267.
 27. STONER, A. W. 1986. Cohabitation on algal habitat islands by two hermaphroditic Tanaidacea (Crustacea, Peracarida). *Journal of Crustacean Biology*. 6:719-728.
 28. WIESER, W. 1959. Effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. *Limnology and Oceanography*. 4:181-194.

Updated 2015

Semibalanus cariosus

A thatched barnacle

Phylum: Arthropoda, Crustacea
Class: Thecostraca, Cirripedia
Order: Thoracica, Sessilia
Family: Archaeobalanidae

Taxonomy: *Semibalanus cariosus* originally belonged to the genus *Balanus*. Members of the genus *Semibalanus*, which was described (initially as a subgenus) by Pilsbry in 1916, differ from *Balanus* species with the presence of membranous bases (Newman and Ross 1976). Thus, a common known synonym for *S. cariosus* is *B. cariosus*.

Description

Size: Individuals typically up to 75 mm in diameter (Henry 1940) and 80 mm in height. Size is highly variable, especially in cylindrical specimens on vertical surfaces, but is not limited by mechanical factors of a wave swept environment (Denny et al. 1985). For example, individuals from Puget Sound, Washington can grow to 100 mm high while only 15 mm in diameter (Pilsbry 1916).

Color: Shell dirty white, gray with round or uncrowded specimens chalky white. Tergum beak can be purple (Pilsbry 1916) and cirri are brown to almost black.

General Morphology: Members of the Cirripedia, or barnacles, can be recognized by their feathery thoracic limbs (called cirri) that are used for feeding. There are six pairs of cirri in *S. cariosus*. Sessile barnacles are surrounded by a **shell** that is composed of a flat **basis** attached to the substratum, a **wall** formed by several articulated **plates** and movable **opercular valves** including **terga** and **scuta** (Newman 2007).

Shell:

Shape: Conical when isolated (Fig. 2), but can be cylindrical if crowded (see Fig. 108, Kozloff 1993).

Basis: Calcareous and flat, attached to hard substrate, rendering *S. cariosus* a sessile, or attached barnacle (Balanomorpha). Basis in *S. cariosus* is membraneous, in contrast to most barnacles which have calcareous bases (Cornwall 1951) and base forms unique starry pattern (Fig. 1), especially in juveniles (Fig. 3) (Ricketts and Calvin 1971).

Wall: Formed by plates and is thick when isolated, but thinner when crowded. The internal surface is usually with faint ribs or wrinkled texture (Cornwall 1951) (Fig. 4).

Longitudinal Tubes: Within walls, tubes are irregular (Fig. 4) and with cross-septa. They are sometimes filled with powder (Pilsbry 1916).

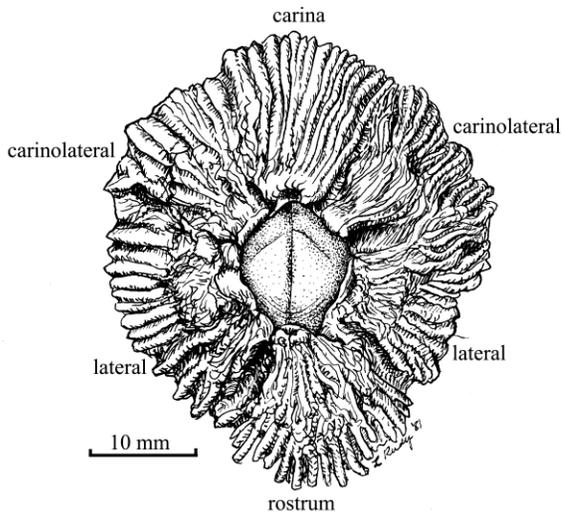
Plates: Six, unequal and calcareous plates bear narrow longitudinal spines, giving specimens a unique thatched appearance (Fig. 1). Each plate is composed of parietes (exposed triangular part), alae (overlapping plate edges) and radii (the plate edge marked off from the parietes by a definite change in direction of growth lines) (Newman 2007). The plates themselves include the rostrum, opposite it the carina and between the carina and rostrum are the four side plates, the carinolateral and rostralateral plates (see Fig. 3, *Balanus glandula*, this guide). When crowded, cylindrical specimens often lack spines (Cornwall 1977). Rostrum overlaps adjacent lateral plates (see Plate 213, Newman 2007). Radii narrow (Cornwall 1951).

Opercular Valves: Thin (Henry 1942) valves consist of two pairs of movable plates inside the wall, which close the aperture: the tergum and the scutum (Figs. 5, 6).

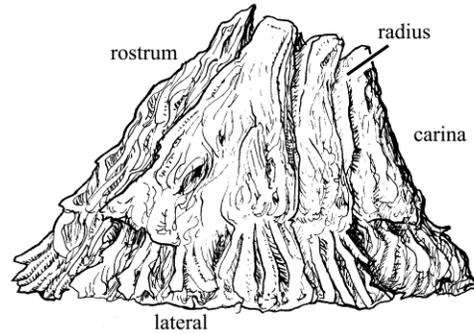
Scuta: Exterior with low growth ridges, the lower ridges are fringed with membrane and usually with a weak longitudinal striation. Interior a small, well-reflexed articular ridge is present, which is continued as a sharp, high, curved adductor ridge (in some specimens, the adductor ridge is very weak). A depressor muscle pit is deep and rather large, often divided by one or two ridges. The occludent margin is with 3–5 oblique coarse teeth (Henry 1940) (Figs. 5a, 6a).

Terga: Very narrow and beaked, with narrow furrow, and long and acute articular ridge. Very narrow and long spur (Pilsbry 1916) that continue as a raised

Semibalanus cariosus



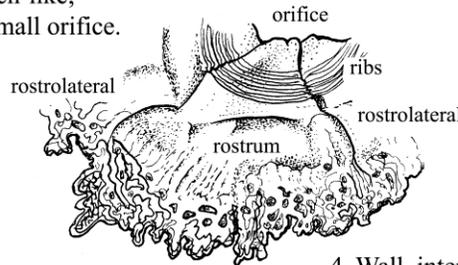
1. *Semibalanus cariosus* (dorsal view, L: 40mm W: 35mm) x2: many long spines: thatch-like; six plates: rostrum overlaps laterals; small orifice.



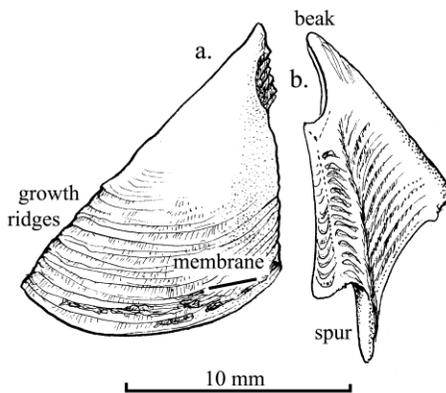
2. Lateral view: conical shape; thick wall; narrow radii .



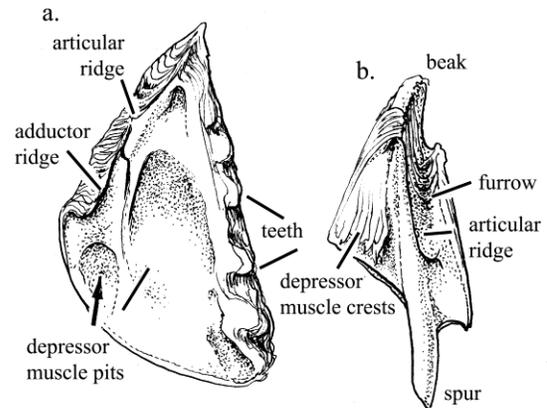
3. Young (dorsal view) x2: star-shaped border; prominent ribs, few in number.



4. Wall, interior (posterior view): basal edges: rostral and lateral plates.



5. Opercular valves, exterior right x4:
 a. scutum: low growth ridges, lower ones membranous; weak longitudinal striations
 b. tergum: narrow, beaked; long spur.



6. Opercular valves, interior x4:
 a. scutum: small, reflexed articular ridge; sharp, high adductor ridge; deep depressor muscle pit; coarse teeth on occludent margin
 b. tergum: narrow furrow; long, acute articular ridge; spur on raised ridge; strong depressor muscle crests.

ridge on the inside with strongly developed depressor muscle crests (Figs. 5b, 6b).

Aperture: The shell opening, from which the cirri emerge when feeding, is controlled by movement of the terga and scuta in conjunction with adductor and depressor muscles. The aperture is small in conical specimens and large in cylindrical ones (Henry 1940), the aperture can be deeply toothed (Fig. 1).

Cirri: Six pairs of conspicuous feathery feeding appendages.

Possible Misidentifications

There are three groups (i.e. superorders) of cirripeds including the Rhizocephala (parasites among crustaceans), the Acrothoracica (shell-less burrowing forms) and the Thoracica. The Thoracica contains 1,000 species worldwide including the monophyletic taxa, Lepadomorpha, the stalked barnacles, and the Balanomorpha, or sessile barnacles (Perez-Losada et al. 2008; Chan et al. 2014). Among the sessile forms, there are four families represented locally. The family Chthamaloidea includes members of the genus *Chthamalus*, which has alae on its rostral plates, not radii. The family Tetraclitoidea has one species locally, *Tetraclita rubescens*, the southern thatched barnacle, that is superficially similar to *S. cariosus*. However, it is characterized by a wall that is composed of four plates (rather than six in the *S. cariosus*). *Tetraclita rubescens* occurs as far north as Monterey Bay, California (Newman 2007).

The remaining two families include the Balanidae and Archaeobalanidae. Balanidae encompasses the genera *Megabalanus*, *Paraconcausus*, and *Menesiniella* (each with one local species), *Amphibalanus* (three local species) and *Balanus* (four local species). The Archaeobalanidae includes the genera *Armatobalanus*, *Conopea*, *Hesperibalanus* and *Semibalanus* (each with one local species). An isolated *S. cariosus*, is with splinter-like spines, nearly black cirri and is not likely to be confused with another barnacle. It has a thatched appearance, being irregularly ribbed and its walls have uneven, longitudinal tubes (Pilsbry 1916). However, where it is crowded or eroded,

these spines may be worn off or not developed, and the barnacle would have to be distinguished from other common barnacles by its tergum and scutum, and by its unique and unusual membraneous base. *Semibalanus cariosus* have terga with a long pointed spur, quite different from either *B. crenatus* or *B. glandula*. *Semibalanus cariosus* commonly co-occurs with *B. crenatus*, *B. glandula*, as well as with *Chthamalus dalli*. Juvenile *S. cariosus* will show a typical heavy ribbing and starry outline, which would distinguish it from young *B. crenatus* or *B. glandula*.

Generally, these latter two species are found higher in the intertidal than is *S. cariosus*, which occurs mostly subtidally.

Balanus crenatus may be easily confused with the ubiquitous *B. glandula*, but is generally found lower in the intertidal. *Balanus glandula* has no longitudinal wall tubes (except when young) and it differs in the structure of terga and scuta: the tergum is very wide and has longer spurs and the scutum has no adductor ridge. *Balanus crenatus*, on the other hand, has a shell wall with a single row of uniformly spaced tubes (Newman 2007). *Balanus trigonus* is a lower intertidal species with a southern distribution (to Monterey Bay, California). *Balanus nubilus*, the giant acorn barnacle, reaches 100 mm in diameter, and has a shell aperture that is relatively large and flaring (Newman 2007). *Balanus nubilus*, would be most likely to be confused with *S. cariosus* at subtidal levels. Both species, as juveniles, have strong ribs: *S. cariosus* has the characteristic starry border (Figs. 1, 3), however, that *B. nubilus* lacks. Both species have a tergal plate with a long spur, but that of *S. cariosus* is pointed, while it is truncate in *B. nubilus* (compare Figs. 5, 6 with Figs. 3b, 4a in *B. nubilus*, this guide). The cirri of *S. cariosus* are also conspicuous and almost black.

Ecological Information

Range: Type locality is the Kurile Islands. Known range includes the Bering Sea south to Morro Bay, California (Newman and Abbott 1980) and Japan. (For range map see Newman and Abbott 1980, p 507.)

Local Distribution: Outer rocky coasts and protected sites in Oregon Bays. In Coos Bay,

also found on floating docks in the Charleston Marina.

Habitat: Hard surface needed for attachment (i.e. rock, shell, wood). Southern specimens prefer protected spots, including deep crevices and overhanging ledges, in the presence of a strong current (Ricketts and Calvin 1971). Puget Sound individuals live exclusively in oceanic conditions. In Coos Bay *S. cariosus* occurs on floating docks (subtidally) just below the water line, versus *B. glandula* that clusters at the water line (e.g. on floats) (Kozloff 1993). An ecosystem engineer, groups of *S. cariosus* (coupled with *Mytilus trossulus*) create necessary microhabitats for other marine invertebrate species (Harley 2011).

Salinity: Collected at salinities of 30 and prefers full-strength seawater.

Temperature: Occurs in temperate waters, with optimal feeding temperatures from 15 to 20 degrees C (Nishizaki and Carrington 2014).

Tidal Level: From high in splash zone (e.g. OIMB Boat House, Coos Bay) to more protected areas farther up bay. Also occurs in the low intertidal zone and subtidally (e.g. floating docks in Charleston). Upper intertidal limit may be determined by desiccation and by substrate temperature as *S. cariosus* and *B. glandula* individuals showed a negative correlation in abundance with substrate temperature in the mid-intertidal (Salish Sea, Washington, Harley 2011). Predation by sea stars may determine lower vertical limit (Cochran et al. 1968).

Associates: Commonly grows below *B. glandula*, a barnacle that is often found growing on *S. cariosus*. Often grows on and amongst *Mytilus californianus*, with *Littorina scutulata* (outer coast) and with *B. crenatus* and the goose barnacle, *Lepas pectinata pacifica* and with masses of tube worms (e.g. *Eudistylia*). Also co-occurs with the barnacles, *Chthamalus dalli* and *Pollicipes polymerus* (outer coast) (Henry 1942).

Abundance: Most common barnacle of low estuarine zone, where the tall and crowded variety can be as dense as 15,000 individuals per square meter (Ricketts and Calvin 1971). The highest density observed locally, at the OIMB Boat House, Coos Head was 270 individuals per 20 square centimeters (Holden 1968).

Life-History Information

Reproduction: Cirripeds usually brood their eggs and *S. cariosus* broods in the winter with larvae hatching in the spring and summer (Newman and Abbott 1980). In Vladivostok, Russia, spawning occurs once a year in November, larvae hatch in March and settlement occurs from April–May (Koch 1989). Individuals are hermaphroditic and self-fertilization is possible (e.g. in isolated individuals), but not common (MacGinitie and MacGinitie 1949; Yonge 1963). Eggs and embryos are retained in ovisacs within the mantle cavity and are discharged as nauplii after four months (Høeg et al. 1987; Arnsberg 2001). For detailed reproductive anatomy see Høeg et al. (1987).

Larva: Cirriped broods hatch as nauplius larvae and undergo 4–6 naupliar stages, each larger and more setose than the last (Høeg et al. 1987; Arnsberg 2001; Chan et al. 2014). For naupliar setal formulae and antenna morphology, see Branscomb and Vedder 1982. Larvae molt to the second naupliar stage shortly after hatching (Branscomb and Vedder 1982). The generalized cirriped nauplius has a triangular or shield-shaped carapace with frontolateral horns and a conspicuous naupliar eye (Fig. 1, Arnsberg 2001; Figs. 22.1–22.2, Chan et al. 2014). In *S. cariosus*, the nauplius is large and bulky. Naupliar stages 2–3 have a long dorsal thoracic spine and approximate naupliar sizes are 350 µm (stage II), 350 µm (stage III), 450 µm (stage IV), 550 µm (stage V) and 650 µm (stage VI) (Fig. 14, Arnsberg 2001). The final larval stage in cirripeds is called a cyprid, a non-feeding stage that attaches to a substrate by its antennae, secretes a cement and builds the adult calcareous shell (Ricketts and Calvin 1971). Cyprids are oblong and composed of a bivalve shell, six thoracic appendages, a pair of compound eyes and a conspicuous lipid reserve anteriorly (Fig. 3, Arnsberg 2001; Figs. 22.2–22.3, Chan et al. 2014). Cyprids prefer rough surfaces for settlement (Yonge 1963). Cyprid larvae in *S. cariosus* are found in plankton in the spring and summer. They are large (960–1200 µm) and with smooth carapace, bear no pigment spots (compare to *Balanus crenatus*, this guide), and are angular both anteriorly and posteriorly (Fig. 15, Arnsberg 2001). Cyprids tend to settle into dark crevices from April–

June (San Juan Archipelago, Washington, Høeg et al. 1987). Like other marine invertebrate larvae, the cyprid larvae of *S. cariosus* and *B. glandula* become concentrated in convergence zones over internal waves, which provides a mechanism for shoreward transport of larvae prior to settlement (Shanks and Wright 1987).

Juvenile: Usually up to 10 mm, juveniles are star-shaped and with 2–3 prominent ribs on carina, one on carinolateral and three or four on lateral and rostrum. Orifice very small (Henry 1940) and surrounded by numerous fine setae in newly metamorphosed individuals. Young juveniles occurs from May to November (Puget Sound, Washington, Høeg et al. 1987).

Longevity: Longevity ranges from three years in low intertidal (Ricketts and Calvin 1971) to 10–15 years (Newman and Abbott 1980).

Growth Rate: Cirriped body growth occurs in conjunction with molting (Kuris et al. 2007). Shell growth depends on barnacle density (e.g. crowded individuals tend to be tall and columnar).

Food: Filter and suspension feeder, eating plankton and detritus that is strained by cirri.

Predators: Heavily preyed upon by sea stars (e.g. *Pisaster*), particularly in its lower range (Cochran 1968). Other predators include the nemertean *Emplectonerna gracile*, birds (e.g. *Larus glaucescens*, *Haematopus bachmani*, *Corvus caurinus*, Wootton 1997), and the whelk, *Nucella freycineti* (Noda 2004). Three snail species, *Thais emarginata*, *Thais canaliculata* and *Thais lamellosa* are also common predators of *B. glandula* and *S. cariosus* (Washington, Connell 1970; Sebens and Lewis 1985). Furthermore, it has been suggested that predation by this genus of drilling gastropods has driven the evolution of balanomorph barnacle plate morphology (Palmer 1982).

Behavior: Barnacles detect changes in light with photoreceptors in simple eyes and in *S. cariosus*, the medial ocellus contains 6–9 photoreceptors (Millecchia and Gwilliam 1972). Furthermore, cirral beating in *S. cariosus* appears to be photoperiodic, where cirral activity is higher at night than during the day (Takeda et al. 1998).

Bibliography

1. ARNSBERG, A. J. 2001. Arthropoda, Cirripedia: The Barnacles. *In: An identification guide to the larval marine invertebrates of the Pacific Northwest*. A. L. Shanks (ed.). Oregon State University Press.
2. BRANSCOMB, E. S., and K. VEDDER. 1982. A description of the naupliar stages of the barnacles *Balanus glandula* (Darwin), *Balanus cariosus* (Pallas), and *Balanus crenatus* (Bruguere) (Cirripedia, Thoracica). *Crustaceana*. 42:83-95.
3. CHAN, B. K. K., J. T. HØEG, and R. KADO. 2014. Thoracica, p. 116-124. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
4. COCHRAN, T. 1968. Effects of predation upon the intertidal cirriped population. Vol. Summer, Book 1. OIMB (ed.), Charleston, OR.
5. COCHRAN, T., M. PATTERSON, H. HOLDEN, and S. STRASSER. 1968. Factors involved in the distribution of three intertidal species of barnacle, Coast Guard Station, Charleston, Oregon. Vol. Summer Book 1. OIMB (ed.), Charleston, OR.
6. CONNELL, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of Thais. *Ecological Monographs*. 40:49-78.
7. CORNWALL, I. E. 1951. Arthropoda: Cirripedia. *In: Canadian Pacific Fauna*. University of Toronto Press for the Fisheries Research Board of Canada, Toronto.
8. —. 1977. The Barnacles of British Columbia. British Colonial Provincial Museum, Victoria.
9. DENNY, M. W., T. L. DANIEL, and M. A. R. KOEHL. 1985. Mechanical limits to size in wave-swept organisms. *Ecological Monographs*. 55:69-102.
10. HARLEY, C. D. G. 2011. Climate change, keystone predation, and biodiversity loss. *Science*. 334:1124-1127.
11. HENRY, D. P. 1940. The Cirripedia of Puget Sound with a key to the

- species. University of Washington Publications in Oceanography. 4:1-48.
12. —. 1942. Studies on the sessile Cirripedia of the Pacific coast of North America. University of Washington Publications in Oceanography. 4:95-134.
 13. HOLDEN, B. 1968. Distributions of three species of barnacles, *Balanus cariosus*, *Balanus glandula* and *Mitella polymerus*. Vol. Summer Book 1. OIMB (ed.), Charleston, OR.
 14. HØEG, J. T., P. L. LIIG, R. R. STRATHMANN, and D. S. WETHEY. 1987. Phylum Crustacea, class Maxillopoda, subclass Cirripedia, p. 370-392. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle.
 15. KOCH, O. M. 1989. Reproduction of the barnacle *Semibalanus cariosus* in the Sea of Japan. *Biologiya Morya*:40-48.
 16. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 17. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 18. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 19. MILLECCHIA, R., and G. F. GWILLIAM. 1972. Photoreception in a barnacle: electrophysiology of the shadow reflect pathway in *Balanus cariosus*. *Science*. 177:438-440.
 20. NEWMAN, W. A. 2007. Cirripedia, p. 475-484. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley.
 21. NEWMAN, W. A., D. P. ABBOTT, R. H. MORRIS, and E. C. HADERLIE. 1980. Cirripedia: The Barnacles. *In*: Intertidal invertebrates of California. Stanford University Press, Stanford, California.
 22. NEWMAN, W. A., and A. ROSS. 1976. Revision of the balanomorph barnacles including a catalog of the species. San Diego Society of Natural History, San Diego.
 23. NISHIZAKI, M. T., and E. CARRINGTON. 2014. Temperature and water flow influence feeding behavior and success in the barnacle *Balanus glandula*. *Marine Ecology Progress Series*. 507:207-218.
 24. NODA, T. 2004. Large-scale variability in recruitment of the barnacle *Semibalanus cariosus*: its cause and effects on the population density and predator. *Marine Ecology Progress Series*. 278:241-252.
 25. PALMER, A. R. 1982. Predation and parallel evolution: recurrent parietal plate reduction in Balanomorph barnacles. *Paleobiology*. 8:31-44.
 26. PEREZ-LOSADA, M., M. HARP, J. T. HOEG, Y. ACHITUV, D. JONES, H. WATANABE, and K. A. CRANDALL. 2008. The tempo and mode of barnacle evolution. *Molecular Phylogenetics and Evolution*. 46:328-346.
 27. PILSBRY, H. A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. U.S. National Museum Bulletin. 93:1-366.
 28. RICKETTS, E. F., and J. CALVIN. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
 29. SEBENS, K. P., and J. R. LEWIS. 1985. Rare events and population structure of the barnacle *Semibalanus cariosus* (Pallas, 1788). *Journal of Experimental Marine Biology and Ecology*. 87:55-65.
 30. SHANKS, A. L., and W. G. WRIGHT. 1987. Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the

- settling rate of intertidal barnacles.
Journal of Experimental Marine
Biology and Ecology. 114:1-13.
31. TAKEDA, S., Y. SHIMOKAWA, and O. MURAKAMI. 1998. Daily activity of the barnacle, *Semibalanus cariosus* (Pallas). Crustaceana. 71:299-311.
 32. WOOTTON, J. T. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and impact of intertidally foraging birds. Ecological Monographs. 67:45-64.
 33. YONGE, C. M. 1963. The Sea shore. Atheneum, New York.

Updated 2015

Balanus crenatus

The crenulated barnacle

Phylum: Arthropoda, Crustacea
Class: Cirripedia
Order: Thoracica, Sessilia
Family: Balanidae

Description

Size: Small, rarely more than 13 mm in diameter (Cornwall 1977). Average size is approximately 14 mm (Cornwall 1951) with the largest individual recorded with diameter of 28 mm (Henry 1940).

Color: White with yellowish epidermis (Cornwall 1977) and exterior without colored markings (Newman 2007). Feeding cirri and penis are cream in color, with the rest of the body being rust-colored.

General Morphology: Members of the Cirripedia, or barnacles, can be recognized by their feathery thoracic limbs (called cirri) that are used for feeding. There are six pairs of cirri in *B. crenatus* (Fig. 2). Sessile barnacles are surrounded by a **shell** that is composed of a flat **basis** attached to the substratum, a **wall** formed by several articulated **plates** (six in *Balanus* species) and movable **opercular valves** including a **terga** and **scuta** (Newman 2007) (Figs. 1, 3, 5).

Shell: Shell can be rough or smooth and varies greatly (Henry 1940), but is usually more smooth than the similar species *B. glandula* (Kozloff 1993). Alaskan species are generally ridged while Oregon specimens are smoother (see Fig. 51, Kozloff 1993).

Shape: Usually broader than tall (Kozloff 1993). Conical, but can be cylindrical if crowded in hummocks, where shape and growth depends on an individual's position within the hummock (e.g. Plate 3, Barnes and Powell 1950).

Basis: Calcareous and flat, attached to hard substrate, rendering *B. crenatus* a sessile, or attached barnacle (Balanomorpha)

Wall: Formed by six unequal plates. The carinal edge of the wall projects forward over the base (Fig. 3) with radii narrow and internal surface of wall ribbed horizontally (Fig. 4). Lower inner wall can be ribbed, smooth, rough, or plicated (Henry 1940).

Longitudinal Tubes: Present within walls and visible if wall is broken (Fig. 4). Tubes occur in a single row and are uniformly spaced (Newman 2007). Some specimens

can have cross-septa in the upper part of the wall.

Plates: Calcareous, nearly conical and columnar. Six in family Balanidae. Each plate is composed of parietes (exposed triangular part), alae (the overlapping plate edges) and radii (the plate edge marked off from the parietes by a definite change in direction of growth lines) (Newman 2007). The plates themselves include the rostrum, opposite it the carina and between the carina and rostrum are the four side plates, the carinolateral and rostrilateral plates (see Fig. 3, *Balanus glandula*, this guide).

Opercular Valves: One pair of scuta opposite the rostrum and a pair of terga at carinal end of orifice (Fig. 1). Growth lines in both valves are not highly prominent. Variation in valve morphology (e.g. smooth and thin versus rough and cylindrical) may be due to habitat (Barnes and Healy 1969).

Scuta: Lacks adductor ridge, is small with flattened beaks (not peaked), and a shallow adductor muscle pit with a well-developed articular ridge (Fig. 5b).

Terga: A short spur that is wider than long and occupies at least ½ of basal margin (Newman 2007). A long, high, articular ridge is present with a deep furrow beside it (Fig. 5a) (Henry 1942).

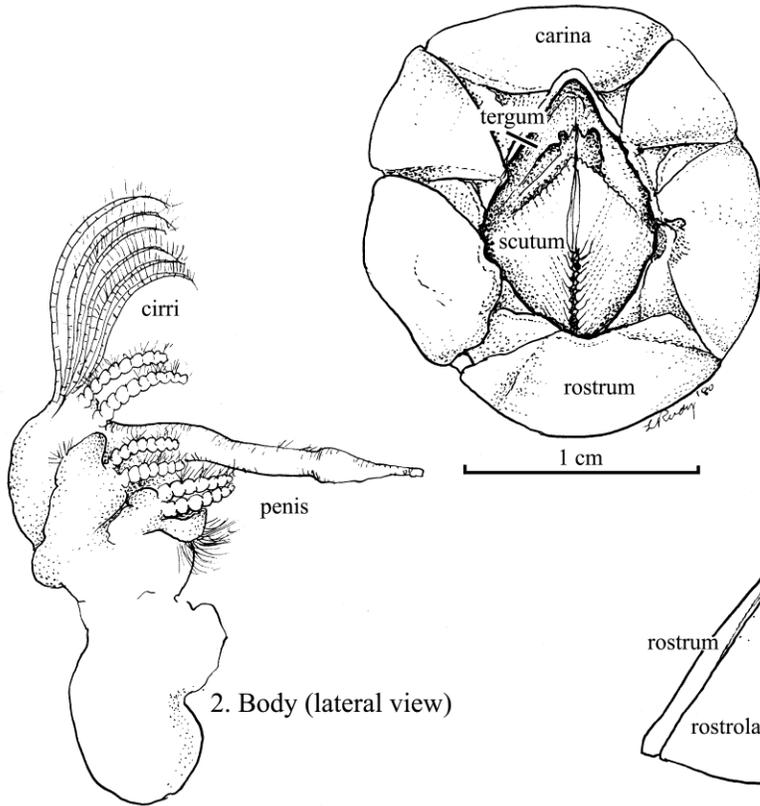
Aperture: A large, rhomboidal orifice, from which the cirri emerge when feeding, is controlled by movement of the terga and scuta in conjunction with adductor and depressor muscles (Fig. 1). The internal edge projects inward in some specimens (Pilsbry 1916). When closed, plates produce a less sinuous line than is present in *B. glandula* (Kozloff 1993).

Cirri: Six pairs of feathery cirri are conspicuous (Fig. 2) and cream in color.

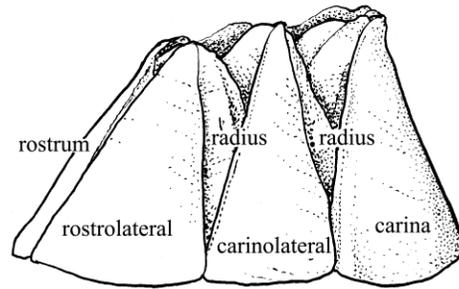
Possible Misidentifications

There are three groups (i.e. superorders) of cirripeds including the Rhizocephala, (parasites among crustaceans), the Acrothoracica (shell-less burrowing forms)

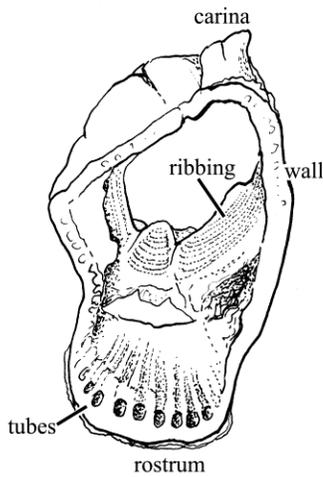
Balanus crenatus



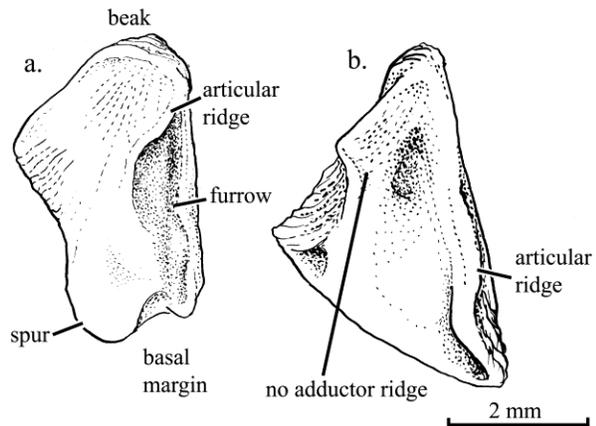
1. *Balanus crenatus* x4:
actual diameter 17 mm
six plates; rostrum overlaps
rostromedials; orifice large,
rhomboidal; opercular valves
(tergum, scutum) in pairs; exterior
smooth.



3. Lateral view x4:
narrow radii.



4. Posterior view x4:
wall: single row longitudinal tubes
horizontal ribbing, upper walls.



5. Opercular valves x12:
a. tergum, right, interior beak flat;
spur half width basal margin;
b. scutum, right, interior
strong articular ridge, no adductor
ridge.

and the Thoracica. The Thoracica contains 1,000 species worldwide including the monophyletic taxa, Lepadomorpha, the stalked barnacles, and the Balanomorpha, or sessile barnacles (Perez-Losada et al. 2008; Chan et al. 2014). Among the sessile forms, there are four families represented locally. The family Chthamaloidea includes members of the genus *Chthamalus*, which has alae on its rostral plates, not radii. *Chthamalus dalli* is found both with and at higher tide levels than *B. glandula*, and individuals are usually brown. The family Tetraclitoidea has one species locally (*Tetraclita rubescens*) and is characterized by a wall that is composed of four plates (rather than six in the Balanidae).

The remaining two families include the Balanidae and Archaeobalanidae. The Archaeobalanidae includes the genera *Armatobalanus*, *Conopea*, *Hesperibalanus* and *Semibalanus* (each with one local species). The latter genus includes a common local intertidal species *S. cariosus* (and former member of the genus *Balanus*). An isolated *S. cariosus*, is with splinter-like spines, nearly black cirri and is not likely to be confused with another barnacle. It has a thatched appearance, being irregularly ribbed and its walls have uneven, longitudinal tubes (Pilsbry 1916). However, where it is crowded or eroded, these spines may be worn off or not developed, and the barnacle would have to be distinguished from other common barnacles by its terga and scuta, and by its unique and unusual membraneous base. *Semibalanus cariosus* have terga with a long pointed spur, quite different from either *B. crenatus* or *B. glandula*. *Semibalanus cariosus* commonly co-occurs with *B. crenatus*, *B. glandula*, as well as with *Chthamalus dalli*. Juvenile *S. cariosus* will show a typical heavy ribbing and starry basis outline, which would distinguish it from young *B. crenatus* or *B. glandula*. Generally, these latter two species are found higher in the intertidal than *S. cariosus*, which occurs mostly subtidally.

Balanidae encompasses the genera *Megabalanus*, *Paraconcaus*, and *Menesiniella* (each with one local species), *Amphibalanus* (three local species) and *Balanus* (four local species). *Balanus crenatus* is generally found in the intertidal

at a lower level than the ubiquitous and morphologically similar *B. glandula*. *Balanus glandula* has no longitudinal wall tubes (except when young) and it differs in the structure of terga and scuta: the terga are very wide and have longer spurs and the scuta have no adductor ridge (compare Fig. 5 with *B. glandula* Figs. 4, 5, this guide). *Balanus crenatus*, on the other hand, has a shell wall with a single row of uniformly spaced tubes (Newman 2007). *Balanus crenatus* is a difficult barnacle to identify: "Not only does every external character vary greatly in this species, but the internal parts very often vary to a surprising degree, and to add to the difficulty, groups of specimens do not rarely vary in the same manner" (Charles Darwin in Cornwall 1951). *Balanus nubilis*, the giant acorn barnacle, is easily distinguished from *B. glandula* by its large size, reaching 100 mm in diameter, and a shell aperture that is relatively large and flaring (Newman 2007). *Balanus trigonus* is a lower intertidal species with a southern distribution (to Monterey Bay, California).

Ecological Information

Range: Type locality is the English coast. Known range includes the North Atlantic and Pacific from the Bering Sea to Santa Barbara, California. *Balanus crenatus* is a common species in the fossil record.

Local Distribution: Protected waters of most northwest bays including many sites in and around Coos Bay.

Habitat: Suitable substrates include pilings, worm tubes, mollusk and crab shells, boat bottoms, wood and other hard substrates (Kozloff 1993). Individuals also often occur amongst eelgrass and debris.

Salinity: Collected at salinities of 30 and is usually found in full-strength seawater, although individuals were found on Vancouver Island in brackish water (Henry 1942).

Temperature: Found in cold and temperate waters.

Tidal Level: Low intertidal down to 165 meters, but is usually from shallower waters along Pacific coasts (Pilsbry 1916).

Associates: Co-occurs with other barnacle species including *B. glandula*, *S. cariosus* (British Columbia, Canada, Cornwall 1977),

and *Chthamalus dalli* (Puget Sound, Washington, Henry 1940). In mud and eelgrass, associates include amphipods, littorine snails, isopods, *B. glandula*, and the mussel, *Mytilus edulis* (South Slough). Readily settles on recently dead *Ensis americanus* shells (internal and external shell portions) (Donovan et al. 2013).

Abundance: Quite common (Cornwall 1951) among the sessile barnacles and may be the most common of all invertebrates on rocky shores (Yonge 1963).

Life-History Information

Reproduction: Cirripeds usually brood their eggs and *B. crenatus* has two broods per year, even at the southern edge of range (Barnes and Powell 1953). Individuals are hermaphroditic and self-fertilization is possible, but not common (Pilsbry 1916; MacGinitie and MacGinitie 1949; Yonge 1963). Eggs and embryos are retained in ovisacs within the mantle cavity and are discharged as nauplii after four months (Høeg et al. 1987; Arnsberg 2001). Light does not affect growth, fertilization or embryonic development (Newman and Abbott 1980) and reproduction in *B. crenatus* can occur continuously, but is limited by available food and temperature (17°C) (Crisp and Patel 1969). For detailed reproductive anatomy see Høeg et al. (1987).

Larva: Cirriped broods hatch as nauplius larvae and undergo 4–6 naupliar stages, each larger and more setose than the last (Høeg et al. 1987; Arnsberg 2001; Chan et al. 2014). For naupliar setal formulae and antenna morphology, see Branscomb and Vedder 1982. Larvae molt to the second naupliar stage shortly after hatching (Branscomb and Vedder 1982). The generalized cirriped nauplius has a triangular or shield-shaped carapace with frontolateral horns and a conspicuous naupliar eye (Fig. 1, Arnsberg 2001; Figs. 22.1–22.2, Chan et al. 2014). In *B. crenatus*, the nauplius carapace is slightly curved anteriorly, between the frontolateral horns (Fig. 9B, Arnsberg 2001). The last three naupliar stages have similar morphology to *Semibalanus cariosus*, but are smaller. To differentiate between species with superficially similar nauplii (e.g. *S. cariosus*, *B. glandula*, *B. crenatus*) see Fig. 9 (Arnsberg 2001). The final larval stage in

cirripeds is called a cyprid, a non-feeding stage that attaches to a substrate by its antennae, secretes a cement (for biochemical composition of cement, see Walker 1972; Naldrett and Kaplan 1997) and builds the adult calcareous shell (Ricketts and Calvin 1971). Cyprids are oblong and composed of a bivalve shell, six thoracic appendages, a pair of compound eyes and a conspicuous lipid reserve anteriorly (Fig. 3, Arnsberg 2001; Figs. 22.2–22.3, Chan et al. 2014). Cyprids prefer rough surfaces for settlement (Yonge 1963), and although algal abundance may positively influence larval settlement in other barnacle species (Strathmann et al. 1981), *B. crenatus* individuals settle on clean surfaces (Hudon et al. 1983). Cyprid larvae in *B. crenatus* have a rounded posterior and a ventral margin that is straight. The carapace is shiny and smooth, with one pair of distinct black pigment spots just posterior to the eyes and is larger than the congener *B. glandula* at 700–960 µm in length (Fig. 10, Arnsberg 2001). The cyprids of *B. crenatus* are most similar to those of *B. nubilus*, but they have a narrower anterior, a distinct evenly curved posterodorsal margin, and black pigment carapace spots (Arnsberg 2001). Larval duration is approximately 2–3 weeks in the plankton (Newman and Abbott 1980) and metamorphosis occurs between 14 and 62 hours after initial attachment to substrate (Meadow 1969). Settlement is dependent on biological, chemical and physical cues as well as the presence of conspecifics with over 30% of settlement occurring on adult shells (Miron et al. 1996).

Juvenile:

Longevity:

Growth Rate: Shell growth in *B. crenatus* is highly dependent on whether individuals are crowded in dense hummocks or solitary (Barnes and Powell 1950). Individuals measured on settlement plates reached near their maximum size (rostrum-carinal length of 20–25 mm) within the first growing season (Millport, United Kingdom, Barnes and Powell 1953). In the first three months after metamorphosis, growth rate ranges between 0.1 and 3.9 mm per month (Meadow 1969). Body growth occurs in conjunction with molting, as is seen in other crustaceans (Kuris et al. 2007).

Food:

Predators:**Behavior:****Bibliography**

1. ARNSBERG, A. J. 2001. Arthropoda, Cirripedia: The Barnacles. *In: An identification guide to the larval marine invertebrates of the Pacific Northwest*. A. L. Shanks (ed.). Oregon State University Press.
2. BARNES, H., and M. J. R. HEALY. 1969. Biometrical studies on some common cirripedes. II. Discriminate analysis of measurements on the scuta and terga of *Balanus balanus*, *Balanus crenatus*, *Balanus improvisus*, *Balanus glandula* and *Balanus amphitrite stuttsburi*, *Balanus pallidus stuttsburi*. *Journal of Experimental Marine Biology and Ecology*. 4:51-70.
3. BARNES, H., and H. T. POWELL. 1950. The development, general morphology and subsequent elimination of barnacle populations. *Balanus crenatus* and *B. balanoides*, after a heavy initial settlement. *Journal of Animal Ecology*. 19:175-179.
4. —. 1953. The growth of *Balanus balanoides* (L.) and *B. crenatus* (Brug.) under varying conditions of submersion. *Journal of the Marine Biological Association of the United Kingdom*. 32:107-127.
5. BRANSCOMB, E. S., and K. VEDDER. 1982. A description of the naupliar stages of the barnacles *Balanus glandula* (Darwin), *Balanus cariosus* (Pallas), and *Balanus crenatus* (Bruguiere) (Cirripedia, Thoracica). *Crustaceana*. 42:83-95.
6. CHAN, B. K. K., J. T. HØEG, and R. KADO. 2014. Thoracica, p. 116-124. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
7. CORNWALL, I. E. 1951. Arthropoda: Cirripedia. *In: Canadian Pacific Fauna*. University of Toronto Press for the Fisheries Research Board of Canada, Toronto.
8. —. 1977. The Barnacles of British Columbia. British Colonial Provincial Museum, Victoria.
9. CRISP, D. J., and B. PATEL. 1969. Environmental control of the breeding of three boreo Arctic cirripedes *Balanus balanoides*, *Balanus balanus*, *Balanus crenatus*. *Marine Biology* (Berlin). 2:283-295.
10. DONOVAN, S. K., L. COTTON, C. VAN DEN ENDE, G. SCOGNAMIGLIO, and M. ZITTERSTEIJN. 2013. Taphonomic significance of a dense infestation of *Ensis americanus* (Binney) by *Balanus crenatus* (Brugiere), North Sea. *Palaios*. 28:837-838.
11. HENRY, D. P. 1940. The Cirripedia of Puget Sound with a key to the species. University of Washington Publications in Oceanography. 4:1-48.
12. —. 1942. Studies on the sessile Cirripedia of the Pacific coast of North America. University of Washington Publications in Oceanography. 4:95-134.
13. HUDON, C., E. BOURGET, and P. LEGENDRE. 1983. An integrated study of the factors influencing the choice of the settling site of *Balanus crenatus* cyprid larvae. *Canadian Journal of Fisheries and Aquatic Sciences*. 40:1186-1194.
14. HØEG, J. T., P. L. LIIG, R. R. STRATHMANN, and D. S. WETHEY. 1987. Phylum Crustacea, class Maxillopoda, subclass Cirripedia, p. 370-392. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle.
15. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
16. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to*

- Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
17. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 18. MEADOWS, P. S. 1969. Settlement, growth and competition in sub littoral populations of barnacles. *Hydrobiologia*. 33:65-92.
 19. MIRON, G., E. BOURGET, and P. ARCHAMBAULT. 1996. Scale of observation and distribution of adult conspecifics: Their influence in assessing passive and active settlement mechanisms in the barnacle *Balanus crenatus* (Brugiere). *Journal of Experimental Marine Biology and Ecology*. 201:137-158.
 20. NALDRETT, M. J., and D. L. KAPLAN. 1997. Characterization of barnacle (*Balanus eburneus* and *B. crenatus*) adhesive proteins. *Marine Biology*. 127:629-635.
 21. NEWMAN, W. A. 2007. Cirripedia, p. 475-484. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley.
 22. NEWMAN, W. A., D. P. ABBOTT, R. H. MORRIS, and E. C. HADERLIE. 1980. Cirripedia: the barnacles. *In: Intertidal invertebrates of California*. Stanford University Press, Stanford, California.
 23. PEREZ-LOSADA, M., M. HARP, J. T. HOEG, Y. ACHITUV, D. JONES, H. WATANABE, and K. A. CRANDALL. 2008. The tempo and mode of barnacle evolution. *Molecular Phylogenetics and Evolution*. 46:328-346.
 24. PILSBRY, H. A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. *U.S. National Museum Bulletin*. 93:1-366.
 25. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 26. STRATHMANN, R. R., E. S. BRANSCOMB, and K. VEDDER. 1981. Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. *Oecologia*. 48:13-18.
 27. WALKER, G. 1972. Biochemical composition of cement of two barnacle species, *Balanus hameri* and *Balanus crenatus*. *Journal of the Marine Biological Association of the United Kingdom*. 52:429-435.
 28. YONGE, C. M. 1963. *The Sea shore*. Atheneum, New York.

Updated 2015

Balanus glandula

Acorn barnacle

Phylum: Arthropoda, Crustacea
Class: Thecostraca, Cirripedia
Order: Thoracica, Sessilia
Family: Balanidae

Description

Size: Up to 3 cm in diameter, but usually less than 1.5 cm (Ricketts and Calvin 1971; Kozloff 1993).

Color: Shell usually white, often irregular and color varies with state of erosion. Cirri are black and white (see Plate 11, Kozloff 1993).

General Morphology: Members of the Cirripedia, or barnacles, can be recognized by their feathery thoracic limbs (called cirri) that are used for feeding. There are six pairs of cirri in *B. glandula* (Fig. 1). Sessile barnacles are surrounded by a **shell** that is composed of a flat **basis** attached to the substratum, a **wall** formed by several articulated **plates** (six in *Balanus* species, Fig. 3) and movable **opercular valves** including **terga** and **scuta** (Newman 2007) (Figs. 2, 4, 5).

Shell:

Shape: Shell surrounding the barnacle body is pyramidal in shape (see Fig. 99, Kozloff 1993) (Fig. 2).

Basis: Calcareous and flat, attached to hard substrate, rendering *B. glandula* a sessile, or attached barnacle (Balanomorpha).

Wall: Formed by the six plates (Fig. 2) and composed of irregular, vertical, filled tubes, giving the exterior the appearance of rough ribbing.

Longitudinal Tubes: Only present in immature individuals (Newman 2007).

Plates: Calcareous, nearly conical and columnar. Six in family Balanidae. Each plate is composed of parietes (exposed triangular part) (Figs. 3a, 3b), alae (the plate overlapping plate edges) and radii (the plate edge marked off from the parietes by a definite change in direction of growth lines) (Fig. 3b) (Newman 2007). The plates themselves include the rostrum, opposite it the carina and between the carina and rostrum are the four side plates, the carinolateral and rostralateral plates (see Plate 213, Newman 2007).

Opercular Valves: Valves consist of two pairs of movable plates inside the wall, which close the aperture: the tergum and the scutum (Figs. 3a, 4, 5).

Terga: The terga are the upper, smaller plate pair and each tergum has a short spur at its base (Fig. 4), deep crests for depressor muscles, a prominent articular ridge, and an articular furrow (Pilsbry 1916).

Scuta: The scuta have pits on either side of a short adductor ridge (Fig. 5), fine growth ridges, and a prominent articular ridge.

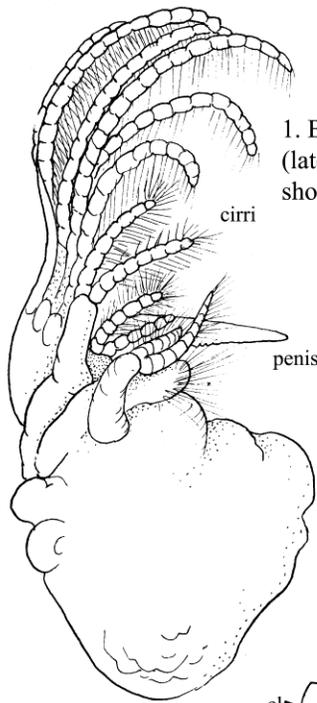
Aperture: The shell opening, from which the cirri emerge when feeding, is controlled by movement of the terga and scuta in conjunction with adductor and depressor muscles. When closed, plates produce a distinct and sinuous line at their junction in *B. glandula* (Kozloff 1993).

Cirri: Feathery, black and white and conspicuous. Each of the six pairs of legs (=cirri), bears 4–7 pairs of setae (Nishizaki and Carrington 2014). The cirri of *B. glandula* were the first observed to exhibit ecophenotypic plasticity, where individuals adjusted response time (i.e. cirral withdrawal) to specific habitats. An adjustment from one habitat (e.g. wave-exposed) to the next (e.g. protected) occurred over a period of two molts (approximately 18 days) (Marchinko 2003).

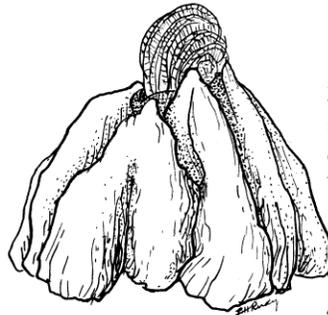
Possible Misidentifications

There are three groups (i.e. superorders) of cirripeds including the Rhizocephala (parasites among crustaceans), the Acrothoracica (shell-less burrowing forms), and the Thoracica. The Thoracica contains 1,000 species worldwide including the monophyletic taxa, Lepadomorpha, the stalked barnacles, and the Balanomorphs, or sessile barnacles (Perez-Losada et al. 2008; Chan et al. 2014). Among the sessile forms, there are four families represented locally. The family Chthamaloidea includes

Balanus glandula

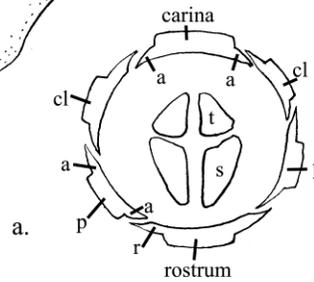


1. Body (lateral view): showing six pairs cirri.

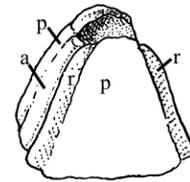


2. *Balanus glandula* x5: size: to 1.5 cm; six plates; color: white, walls eroded, black and white cirri.

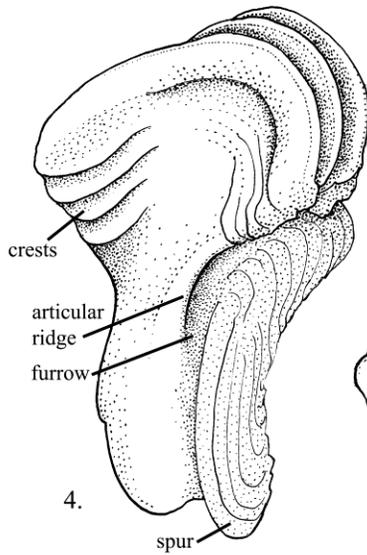
5 cm



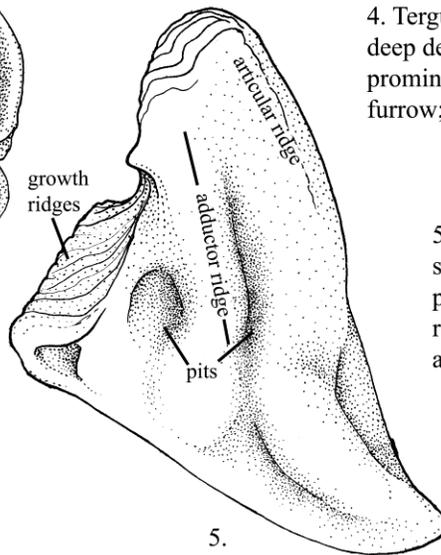
3. Plate arrangement (schematic cross-section) in Balanidae, rostrum overlaps lateral plates; t=tergum, s=scutum, r=radius, a=ala, p=paries, cl=carinolateral, l=lateral (Smith and Carlton, 1975).



b.



4.



5.

4. Tergum: deep depressor muscle crests; prominent articular ridge and furrow; short spur.

5. Scutum: short adductor ridge with pit on each side; fine growth ridges, (exterior) prominent articular ridge.

members of the genus *Chthamalus*. Juvenile *Balanus glandula* and *Chthamalus dalli*, often found together, are very alike. The genus *Chthamalus* has alae on its rostral plates, not radii (i.e. the rostral plate is overlapped, rather than underlapped, as in *B. glandula*, by the rostrolateral plates). *Chthamalus dalli* is found both with and at higher tide levels than *B. glandula*, and individuals are usually brown. The family Tetraclitoidea has one species locally (*Tetraclita rubescens*), and is characterized by a wall that is composed of four plates (rather than six in the Balanidae).

The remaining two families are the Balanidae and Archaeobalanidae. The Archaeobalanidae includes the genera *Armatobalanus*, *Conopea*, *Hesperibalanus* and *Semibalanus* (each with one local species). The latter genus includes a common local intertidal species *S. cariosus* (and former member of the genus *Balanus*). An isolated *S. cariosus*, is with splinter-like spines, nearly black cirri and is not likely to be confused with another barnacle. It has a thatched appearance, being irregularly ribbed and its walls have uneven, longitudinal tubes (Pilsbry 1916). However, where it is crowded or eroded, these spines may be worn off or not developed, and the barnacle would have to be distinguished from other common barnacles by its terga and scuta, and by its unique and unusual membraneous base. *Semibalanus cariosus* have terga with a long pointed spur, quite different from either *B. crenatus* or *B. glandula*. *Semibalanus cariosus* commonly co-occurs with *B. crenatus*, *B. glandula*, as well as with *Chthamalus dalli*. Juvenile *S. cariosus* will show a typical heavy ribbing and starry basis outline, which would distinguish it from young *B. crenatus* or *B. glandula*. Generally, these latter two species are found higher in the intertidal than is *S. cariosus*, which occurs mostly subtidally.

Balanidae encompasses the genera *Megabalanus*, *Paraconceus*, and *Menesiniella* (each with one local species), *Amphibalanus* (three local species) and *Balanus* (four local species). *Balanus crenatus* is generally found in the intertidal at a lower level than the ubiquitous and morphologically similar *B. glandula*. *Balanus glandula* has no longitudinal wall tubes (except when young) and it differs in the

structure of terga and scuta: the terga are very wide and have longer spurs and the scuta have no adductor ridges (compare Fig. 5 with *B. glandula* Figs. 4, 5, this guide). *Balanus crenatus*, on the other hand, has a shell wall with a single row of uniformly spaced tubes (Newman 2007). *Balanus crenatus* is a difficult barnacle to identify: "Not only does every external character vary greatly in this species, but the internal parts very often vary to a surprising degree, and to add to the difficulty, groups of specimens do not rarely vary in the same manner" (Charles Darwin in Cornwall 1951). *Balanus nubilus*, the giant acorn barnacle, is easily distinguished from *B. glandula* by its large size, reaching 100 mm in diameter, and a shell aperture that is relatively large and flaring (Newman 2007). *Balanus trigonus* is a lower intertidal species with a southern distribution (to Monterey Bay, California).

Ecological Information

Range: Type range includes Alaska to Baja California (Darwin 1854), *B. glandula* was introduced to South America (Argentina) and Japan (Kado 2003; Newman 2007; Rashidul Alam et al. 2014).

Local Distribution: Ubiquitous in a wide variety of locations from the open rocky shores to the salty or brackish bays of the Oregon coast (Kozloff 1993), where populations show genetic heterogeneity over great distances (Barshis et al. 2011), except in central California where gene flow is more restricted between populations (Sotka et al. 2004).

Habitat: Very adaptable to a variety of habitats. Suitable substrates include rocks, pilings, wood, other crustaceans, molluscs, and barnacles. Often in conditions with extreme exposure to sun, wind, rain and can tolerate estuarine conditions quite well, including those of poor water circulation, low oxygen, and little wave action (Ricketts and Calvin 1971). Populations in polluted areas have been shown to exhibit lower genetic diversity, with more individuals of the same haplotype (southern California, Ma et al. 2000).

Salinity: Collected at salinities of 30, but can also survive at lower salinities (Ricketts and Calvin 1971). *Balanus glandula* resists

desiccation better than other *Balanus* species (Newman and Abbott 1980).

Temperature: Survives a wide range of temperatures, but optimal temperatures for feeding range between 10° and 15° C (Nishizaki and Carrington 2014).

Tidal Level: One of the most important zonation indicators as very small barnacles often settle high in the dry uppermost intertidal zone, below *Littorina* (Ricketts and Calvin 1971). Individuals are most common in the high to mid-tide zone (Darwin 1854) and their upper limit appears to be set by substrate temperature as *S. cariosus* and *B. glandula* individuals showed a negative correlation in abundance with substrate temperature in the mid-intertidal (Salish Sea, Washington, Harley 2011).

Associates: Forms dense clusters with *Chthamalus dalli*, *Nucella*, mussels and limpets (including *Lottia digitalis*) at high tide levels (Kozloff 1993; Newman 2007). Sometimes found on larger *Balanus cariosus* individuals.

Abundance: One of the most abundant animals on the coast with up to 70,000 individuals per square meter (Ricketts and Calvin 1971). Larval abundance can also be high in the plankton, where 10 cyprids per 200 liters were reported in central California (Gaines et al. 1985).

Life-History Information

Reproduction: Cirripeds usually brood their eggs and *B. glandula* produces 2–6 broods/year, in winter and spring (Oct–May in southern California), and through September on Vancouver Island and December in Friday Harbor (Høeg et al. 1987). Barnacles are one of the few sessile organisms with internal fertilization and plasticity in penis length has been observed, with shorter penises in high wave-energy environments (Neufeld and Palmer 2008). Individuals are hermaphroditic and self-fertilization is possible, but not common (MacGinitie and MacGinitie 1949; Yonge 1963). Spermcast spawning can occur (Barazandeh et al. 2014). Eggs and embryos are retained in ovisacs within the mantle cavity and are discharged as nauplii after four months (Yonge 1963; Høeg et al. 1987; Arnsberg 2001). Ascorbic acid in water stimulates copulation (R. Boomer personal

communication). For detailed reproductive anatomy see Høeg et al. (1987).

Larva: Cirriped broods hatch as nauplius larvae and undergo 4–6 naupliar stages, each larger and more setose than the last (Høeg et al. 1987; Arnsberg 2001; Chan et al. 2014). Fewer setae occur on the antennae rami and mandibles in *B. glandula* nauplii beyond stage I than is seen in congeners (Brown and Roughgarden 1985). For naupliar setal formulae and antenna morphology, see Branscomb and Vedder 1982. Larvae molt to the second naupliar stage shortly after hatching (Branscomb and Vedder 1982). The generalized cirriped nauplius has a triangular or shield-shaped carapace with frontolateral horns and a conspicuous naupliar eye (Fig. 1, Arnsberg 2001; Figs. 22.1–22.2, Chan et al. 2014). In *B. glandula*, the nauplius has curved frontal horns and a 3-lobed labrum (Brown and Roughgarden 1985; Figs. 4 and 7, Arnsberg 2001). The first naupliar stage lasts less than an hour and stages 4–6 are recognizable by a pair of well-developed dorsal carapace spines (Arnsberg 2001). The sizes of *B. glandula* nauplii begin at 271 µm (stage I) and end at 745 µm (stage VI) (Brown and Roughgarden 1985). The final larval stage in cirripeds is called a cyprid, a non-feeding stage that attaches to a substrate by its antennae, secretes a cement and builds the adult calcareous shell (Ricketts and Calvin 1971). Cyprids are oblong and composed of a bivalve shell, six thoracic appendages, a pair of compound eyes and a conspicuous lipid reserve anteriorly (Fig. 3, Arnsberg 2001; Figs. 22.2–22.3, Chan et al. 2014). Cyprids prefer rough surfaces for settlement (Yonge 1963). Cyprid larvae in *B. glandula* are golden in color and have a distinct carapace shape and surface that is dull and decorated with papillae and four pigment patches, they are 640–780 µm in length and can be observed in the plankton year round except in winter months (Fig. 8, Arnsberg 2001). The pelagic larval duration in *B. glandula* is estimated at 3–4 weeks (Brown and Roughgarden 1985). Larval settlement is effected by degree of coastal upwelling, where more settlement is observed in years when upwelling is weak and larvae stay closer to shore (Connolly and Roughgarden 1998; Barshis et al. 2011). Most larval settlement occurs in spring and

autumn in Friday Harbor, Washington (Høeg et al. 1987), but may vary with sea temperature (e.g. January–June, Santa Barbara, California, Connell 1970). Where cyprids were abundant in the water column, settlement occurred at a rate of 2 cyprids per square centimeter of available space (Gaines et al. 1985). Like other marine invertebrate larvae, the cyprid larvae of *S. cariosus* and *B. glandula* become concentrated in convergence zones over internal waves, which provides a mechanism for shoreward transport of larvae prior to settlement (Shanks and Wright 1987).

Juvenile: Newly metamorphosed juveniles can be found settled in the intertidal from -0.6 meters to -0.3 meters and have six pairs of setae situated near and around the opercular opening (Høeg et al. 1987). The shell wall in juveniles consists of empty vertical tubes, which only become filled and irregular in the adult. Individuals from the upper tidal levels reach sexual maturity and spawn during their second year, while those from lower areas do so in their first year (Yonge 1963).

Longevity: 8–10 years (Newman and Abbott 1980).

Growth Rate: Cirriped body growth occurs in conjunction with molting (Kuris et al. 2007). Shell growth proceeds as follows (basal diameters): 7–12 mm in first year, 10–16 mm by the second year and 14–17 mm by three years (Newman and Abbott 1980). Adults under high densities form “hummocks” where individual barnacles grow tall and form tightly-packed columns (Bertness et al. 1998). Shell size (e.g. terga and scuta) may correlate with temperature (Barnes and Healy 1969). Those *B. glandula* that settle at lowest tidal heights grow fastest in the first year, but after that, those higher in the intertidal exhibit the fastest growth (Yonge 1963).

Food: Filter or suspension feeders (Nishizaki and Carrington 2014), barnacles eat plankton and some detritus, that is strained from incoming currents by several pairs of hydrostatically-extended thoracic appendages called cirri (Fig. 1) (MacGinitie and MacGinitie 1949).

Predators: Snail *Nucella* at low tide levels, as well as sea stars, worms (particularly on juveniles), birds and occasionally humans (e.g. Northwest Native Americas). Three snail species, *Thais emarginata*, *Thais canaliculata*

and *Thais lamellose*, are also common predators of *B. glandula* and *S. cariosus* (Washington, Connell 1970). Furthermore, it has been suggested that predation by this genus of drilling gastropods has driven the evolution of balanomorph barnacle plate morphology (Palmer 1982). Predators on *B. glandula* larvae include many plankton feeders (e.g. fish, MacGinitie and MacGinitie 1949).

Behavior: Adults exhibit anti-predatory hiding behavior (i.e. withdrawal of cirral fan) in response to shadow (Dill and Gillet 1991). Cyprid larvae can actively search out settling area by “walking” on antennules, and adult distribution is at least in part determined by these pre-settlement behaviors and zonation in the plankton (Grosberg 1982; Gaines et al. 1985).

Bibliography

1. ARNSBERG, A. J. 2001. Arthropoda, Cirripedia: the barnacles. *In*: An identification guide to the larval marine invertebrates of the Pacific Northwest. A. L. Shanks (ed.). Oregon State University Press.
2. BARAZANDEH, M., C. S. DAVIS, and A. R. PALMER. 2014. Where even a long penis can't help: evidence of long-distance spermcast mating in two acorn barnacles. *Journal of Experimental Marine Biology and Ecology*. 454:49-54.
3. BARNES, H., and M. J. R. HEALY. 1969. Biometrical studies on some common cirripedes. II. Discriminate analysis of measurements on the scuta and terga of *Balanus balanus*, *Balanus crenatus*, *Balanus improvisus*, *Balanus glandula* and *Balanus amphitrite stuttsburi*, *Balanus pallidus stuttsburi*. *Journal of Experimental Marine Biology and Ecology*. 4:51-70.
4. BARSHIS, D. J., E. E. SOTKA, R. P. KELLY, A. SIVASUNDAR, B. A. MENGE, J. A. BARTH, and S. R. PALUMBI. 2011. Coastal upwelling is linked to temporal genetic variability in the acorn barnacle *Balanus glandula*.

- Marine Ecology Progress Series. 439:139-150.
5. BERTNESS, M. D., S. D. GAINES, and S. M. YEH. 1998. Making mountains out of barnacles: the dynamics of acorn barnacle hummocking. *Ecology*. 79:1382-1394.
 6. BRANSCOMB, E. S., and K. VEDDER. 1982. A description of the naupliar stages of the barnacles *Balanus glandula* (Darwin), *Balanus cariosus* (Pallas), and *Balanus crenatus* (Bruguiere) (Cirripedia, Thoracica). *Crustaceana*. 42:83-95.
 7. BROWN, S. K., and J. ROUGHGARDEN. 1985. Growth, morphology, and laboratory culture of larvae of *Balanus glandula* (Cirripedia, Thoracica). *Journal of Crustacean Biology*. 5:574-590.
 8. CHAN, B. K. K., J. T. HØEG, and R. KADO. 2014. Thoracica, p. 116-124. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
 9. CONNELL, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of Thais. *Ecological Monographs*. 40:49-78.
 10. CONNOLLY, S. R., and J. ROUGHGARDEN. 1998. A latitudinal gradient in northeast Pacific intertidal community structure: Evidence for an oceanographically based synthesis of marine community theory. *American Naturalist*. 151:311-326.
 11. DARWIN, C. 1854. A Monograph of the subclass Cirripedia (Part II Balandiae). Royal Society, London.
 12. DILL, L. M., and J. F. GILLETT. 1991. The economic logic of barnacle *Balanus glandula* (Darwin) hiding behavior. *Journal of Experimental Marine Biology and Ecology*. 153:115-127.
 13. GAINES, S., S. BROWN, and J. ROUGHGARDEN. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia*. 67:267-272.
 14. GROSBERG, R. K. 1982. Intertidal zonation of barnacles: the influence of planktonic zonation of larvae on vertical distribution of adults. *Ecology*. 63:894-899.
 15. HARLEY, C. D. G. 2011. Climate change, keystone predation, and biodiversity loss. *Science*. 334:1124-1127.
 16. HØEG, J. T., P. L. LIIG, R. R. STRATHMANN, and D. S. WETHEY. 1987. Phylum Crustacea, class Maxillopoda, subclass Cirripedia, p. 370-392. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle.
 17. KADO, R. 2003. Invasion of Japanese shores by the NE Pacific barnacle *Balanus glandula* and its ecological and biogeographical impact. *Marine Ecology Progress Series*. 249:199-206.
 18. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 19. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 20. MA, X. L., D. L. COWLES, and R. L. CARTER. 2000. Effect of pollution on genetic diversity in the bay mussel *Mytilus galloprovincialis* and the acorn barnacle *Balanus glandula*. *Marine Environmental Research*. 50:559-563.
 21. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 22. MARCHINKO, K. B. 2003. Dramatic phenotypic plasticity in barnacle legs (*Balanus glandula* (Darwin)): magnitude, age dependence, and speed of response. *Evolution*. 57:1281-1290.

23. NEUFELD, C. J., and A. R. PALMER. 2008. Precisely proportioned: intertidal barnacles alter penis form to suit coastal wave action. *Proceedings of the Royal Society B-Biological Sciences*. 275:1081-1087.
24. NEWMAN, W. A. 2007. Cirripedia, p. 475-484. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley.
25. NEWMAN, W. A., D. P. ABBOTT, R. H. MORRIS, and E. C. HADERLIE. 1980. Cirripedia: the barnacles. *In: Intertidal invertebrates of California*. Stanford University Press, Stanford, California.
26. NISHIZAKI, M. T., and E. CARRINGTON. 2014. Temperature and water flow influence feeding behavior and success in the barnacle *Balanus glandula*. *Marine Ecology Progress Series*. 507:207-218.
27. PALMER, A. R. 1982. Predation and parallel evolution: recurrent parietal plate reduction in Balanomorph barnacles. *Paleobiology*. 8:31-44.
28. PEREZ-LOSADA, M., M. HARP, J. T. HOEG, Y. ACHITUV, D. JONES, H. WATANABE, and K. A. CRANDALL. 2008. The tempo and mode of barnacle evolution. *Molecular Phylogenetics and Evolution*. 46:328-346.
29. PILSBRY, H. A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. U.S. National Museum Bulletin. 93:1-366.
30. RASHIDUL ALAM, A. K. M., T. HAGINO, K. FUKAYA, T. OKUDA, M. NAKAOKA, and T. NODA. 2014. Early phase of the invasion of *Balanus glandula* along the coast of Eastern Hokkaido: changes in abundance, distribution, and recruitment. *Biological Invasions*. 16:1699-1708.
31. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
32. SHANKS, A. L., and W. G. WRIGHT. 1987. Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles. *Journal of Experimental Marine Biology and Ecology*. 114:1-13.
33. SOTKA, E. E., J. P. WARES, J. A. BARTH, R. K. GROSBERG, and S. R. PALUMBI. 2004. Strong genetic clines and geographical variation in gene flow in the rocky intertidal barnacle *Balanus glandula*. *Molecular Ecology*. 13:2143-2156.
34. YONGE, C. M. 1963. *The Sea shore*. Atheneum, New York.

Updated 2015
T.C. Hiebert and M. Jarvis

Balanus nubilus

The giant barnacle

Phylum: Arthropoda, Crustacea
Class: Thecostraca, Cirripedia
Order: Thoracica, Sessilia
Family: Balanidae

Description

Size: Largest barnacle on the Pacific coast, and probably in the world (Ricketts and Calvin 1971), with individuals up to 100 mm in diameter, and nearly as tall (Cornwall 1951). The illustrated specimen (from Coos Bay) is 90 mm in diameter.

Color: Shell dirty white with interior of scuta and terga (see Plate 18, Kozloff 1993) buff and tergal beak usually purple tipped (Cornwall 1951).

General Morphology: Members of the Cirripedia, or barnacles, can be recognized by their feathery thoracic limbs (called cirri) that are used for feeding. There are six pairs of cirri in *B. nubilus*. Sessile barnacles are surrounded by a **shell** that is composed of a flat **basis** attached to the substratum, a **wall** formed by several articulated **plates** (six in *Balanus* species) and movable **opercular valves** including **terga** and **scuta** (Newman 2007) (Figs. 1, 3, 4).

Shell: Exterior can be rugged and worn with well-developed ribs that become eroded with age (Figs. 1, 2) (Cornwall 1977).

Shape: Steeply conical and, like other barnacles, they can become cylindrical when crowded. Young specimens can also be cylindrical (Henry 1940).

Basis: Calcareous and flat, attached to hard substrate, rendering *B. nubilus* a sessile, or attached barnacle (Balanomorpha). Barnacle base is thick, porous at edges and thin at center.

Wall:

Longitudinal Tubes: A single row of tubes is uniform and within shell walls (Ricketts and Calvin 1971).

Plates: Calcareous, nearly conical and columnar. Six in family Balanidae. Each plate is composed of parietes (exposed triangular part), alae (the plate overlapping plate edges) and radii (the plate edge marked off from the parietes by a definite change in direction of growth lines) (Newman 2007). The plates themselves include the rostrum, opposite it the carina and

between the carina and rostrum are the four side plates, the carinolateral and rostrolateral plates (see Fig. 3, *Balanus glandula*, this guide). Internal surfaces with fine horizontal ribbing above and smooth near base, particularly in older specimens (Pilsbry 1916). Radii rather narrow (Darwin 1854).

Opercular Valves: Thick and yellowish, buff on interior but never white. Tergal beaks project above orifice edge (Cornwall 1977). Tergal and scutal adductor and depressor muscles are very thick in *B. nubilus* (2 mm and 1.4 mm, respectively, Hoyle and Smyth 1963).

Scuta: External surface with prominent growth lines, a deep canal from apex and downward in old eroded specimens (Fig. 4b). Internally with low articular ridge that has a very narrow articular furrow. The prominent adductor ridge is large and with a shallow adductor pit.

Terga: Beak triangular and often purple (Fig 4a), especially in older specimens (Cornwall 1951). External growth ridges narrow and regular, with narrow, shallow longitudinal furrow. Internally, numerous depressor muscle crests. Tergal spur is wide at base and tapers to a narrow truncate end (Fig. 4a). Moderate articular ridge is with shallow broad articular furrow (Fig. 4a).

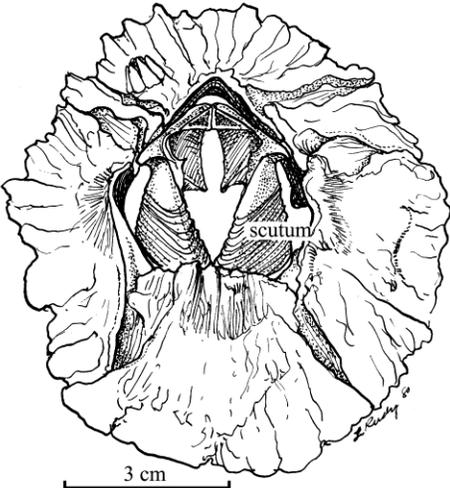
Aperture: Large, flared and with a jagged edge (Cornwall 1977).

Cirri: Six pairs of conspicuous feathery feeding appendages.

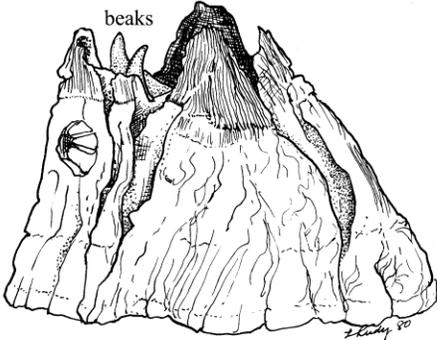
Possible Misidentifications

There are three groups (i.e. superorders) of cirripeds including the Rhizocephala, (parasites among crustaceans), the Acrothoracica (shell-less burrowing forms) and the Thoracica. The Thoracica contains 1,000 species worldwide including the monophyletic taxa, Lepadomorpha, the stalked barnacles, and the Balanomorpha, or sessile barnacles (Perez-Losada et al. 2008; Chan et al. 2014). Among the sessile

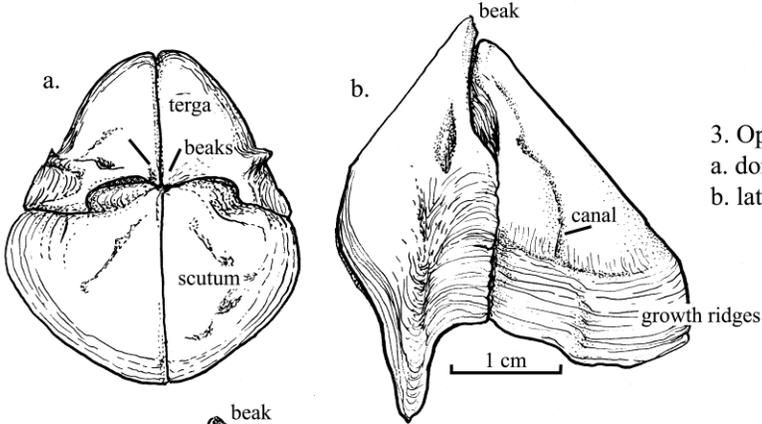
Balanus nubilus



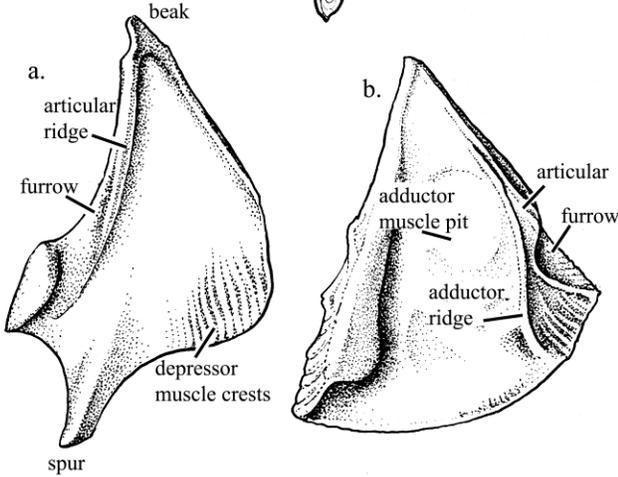
1. *Balanus nubilus* x1:
six plates; ribs eroded;
very large: up to 10 cm diameter.



2. Lateral view:
walls a steep cone, steeply conical;
orifice large, flaring.



3. Opercular plates, exterior x2:
a. dorsal.
b. lateral.



4. Opercular plates, interior
a. scutum.
b. tergum.

forms, there are four families represented locally. The family Chthamaloidea includes members of the genus *Chthamalus*, which has alae on its rostral plates, not radii.

Chthamalus dalli is found both with and at higher tide levels than is *B. glandula*, and individuals are usually brown. The family Tetraclitoidea has one species locally (*Tetraclita rubescens*) and is characterized by a wall that is composed of four plates (rather than six in the Balanidae).

The remaining two families include the Balanidae and Archaeobalanidae. The Archaeobalanidae includes the genera *Armatobalanus*, *Conopea*, *Hesperibalanus* and *Semibalanus* (each with one local species). The latter genus includes a common local intertidal species *S. cariosus* (and former member of the genus *Balanus*). An isolated *S. cariosus*, is with splinter-like spines, nearly black cirri and is not likely to be confused with another barnacle. It has a thatched appearance, being irregularly ribbed: its walls have uneven, longitudinal tubes (Pilsbry 1916). However, where it is crowded or eroded, these spines may be worn off or not developed, and the barnacle would have to be distinguished from other common barnacles by its tergum and scutum, and by its unique and unusual membraneous base. *Balanus nubilus*, would be most likely to be confused with *S. cariosus* at subtidal levels. Both species, as juveniles, have strong ribs. *S. cariosus* has the characteristic starry border, however, that *B. nubilus* lacks. Both species have a tergal plate with a long spur (Figs. 3b, 4a), but that of *S. cariosus* is pointed, while it is truncate in *B. nubilus*. The cirri of *S. cariosus* are conspicuous and almost black.

Balanidae encompasses the genera *Megabalanus*, *Paraconcaucus*, and *Menesiniella* (each with one local species), *Amphibalanus* (three local species) and *Balanus* (four local species). *Balanus nubilus*, is easily distinguished from other species by its large size and a shell aperture that is relatively large and flaring (Newman 2007). *Balanus trigonus* is a lower intertidal species with a southern distribution (to Monterey Bay, California). *Balanus crenatus* is generally found in the intertidal at a lower level than the ubiquitous and morphologically similar *B. glandula*.

Balanus glandula has no longitudinal wall tubes (except when young) and it differs in the structure of terga and scuta: the tergum is very wide and has longer spurs and the scutum has no adductor ridge. *Balanus crenatus*, on the other hand, has a shell wall with a single row of uniformly spaced tubes (Newman 2007).

Ecological Information

Range: Type region is Monterey Bay, California (Cornwall 1951). Known distribution includes the west coast of North America from the southern boundary of Alaska to the mid Baja California coast.

Local Distribution: Common in Coos Bay and at several locations along the South Slough as well as south in Port Orford (Pilsbry 1916).

Habitat: Suitable substrates include pilings in bays with strong tidal action (Cornwall 1951), rocks, shell hash and kelp holdfasts (Cornwall 1977). Largest specimens are observed on fairly exposed wharf pilings where individuals can grow on top of each other to make accretions one foot high (Ricketts and Calvin 1971).

Salinity: Collected at salinities of 30 and no known collections from brackish water.

Balanus nubilus individuals can regulate pH within their muscle fibers, but require external sodium ions to do so (Boron et al. 1981). Considerable research is focused on the physiology and neuroscience of *B. nubilus* (e.g. Hoyle and Smyth 1963; Morris and Lecar 1981; Stockbridge and Ross 1984; Ross et al. 1986; Callaway et al. 1989).

Temperature: From temperate waters.

Tidal Level: From low to shallow waters (3–6 meters) and occasionally to 55 meters (Cornwall 1977).

Associates: Often encrusted with other barnacles, sea stars and anemones on overhanging rocks (British Columbia, Canada, Cornwall 1951). Boring sponges can erode shells (Cornwall 1977). Individuals also occur on boat bottoms with mussels and congeners (MacGinitie and MacGinitie 1949) and is often covered with brown furry mats of the entoproct, *Barentsia* (Pilsbry 1916).

Abundance: The second most common barnacle of the low intertidal zone (most abundant is *Semibalanus cariosus*, Pilsbry 1916). More common in Puget Sound,

Washington and north (Ricketts and Calvin 1971) where individuals characteristically grow in large clumps on rocky bottoms (Henry 1940).

Life-History Information

Reproduction: Cirripeds usually brood their eggs and while individuals are hermaphroditic and, although self-fertilization is possible, cross-fertilization is the rule for gregarious types like *B. nubilus* (MacGinitie and MacGinitie 1949; Yonge 1963). Eggs and embryos are retained in ovisacs within the mantle cavity and are discharged as nauplii after four months (Høeg et al. 1987; Arnsberg 2001). For detailed reproductive anatomy see Høeg et al. (1987).

Larva: Cirriped broods hatch as nauplius larvae and undergo 4–6 naupliar stages, each larger and more setose than the last (Høeg et al. 1987; Arnsberg 2001; Chan et al. 2014). The generalized cirriped nauplius has a triangular or shield-shaped carapace with frontolateral horns and a conspicuous naupliar eye (Fig. 1, Arnsberg 2001; Figs. 22.1–22.2, Chan et al. 2014). In *B. nubilus*, the nauplius is characterized by straight frontolateral horns and a goblet-shaped carapace, in naupliar stages 2–6 (Fig. 11, Arnsberg 2001). The carapace shape in *B. nubilus* is recognizable and makes them easy to identify from other *Balanus* species (Arnsberg 2001). The final larval stage in cirripeds is called a cyprid, a non-feeding stage that attaches to a substrate by its antennae, secretes a cement and builds the adult calcareous shell (Ricketts and Calvin 1971). Cyprids are oblong and composed of a bivalve shell, six thoracic appendages, a pair of compound eyes and a conspicuous lipid reserve anteriorly (Fig. 3, Arnsberg 2001; Figs. 22.2–22.3, Chan et al. 2014). Cyprids prefer rough surface for settlement (Yonge 1963). Cyprid larvae in *B. nubilus* are characterized by a broadly rounded anterior and narrow posterior and a large size (800–1000 µm) (Fig. 12, Arnsberg 2001). The cyprids of *B. crenatus* are most similar to those of *B. nubilus*, but they have a narrower anterior, a distinct evenly curved posterodorsal margin, and black pigment carapace spots (Arnsberg 2001).

Juvenile: Often with cylindrical morphology.

Longevity:

Growth Rate: Cirriped body growth occurs in conjunction with molting (Kuris et al. 2007). Shell growth depends on barnacle density (e.g. crowded individuals tend to be tall and columnar).

Food: Filter and suspension feeder.

Predators: *Balanus* species are usually preyed upon by sea stars (e.g. *Pisaster* species) and by the nemertean *Emplectonema gracile* (Cochran 1968). It has been suggested that predation by *Thais*, a genus of drilling gastropods has influenced plate morphology over evolutionary time in balanomorph barnacles (Palmer 1982).

Behavior: Individuals tend to grow in accretions into deep clusters that often create a heavy clump (i.e. hummock) which falls off substrate and sinks to bottom where animals cannot live. *Balanus nubilus* individuals can detect changes in light with photoreceptors in three simple eyes. A single medial eye contains four photoreceptors, while the two lateral eyes contain three each (Stockbridge and Ross 1984; Callaway et al. 1989).

Bibliography

1. ARNSBERG, A. J. 2001. Arthropoda, Cirripedia: the barnacles, p. 155-175. *In: An identification guide to the larval marine invertebrates of the Pacific Northwest*. A. L. Shanks (ed.). Oregon State University Press.
2. BORON, W. F. 1981. pH regulation in barnacle muscle fibers: dependence on extracellular sodium and bicarbonate. *American Journal of Physiology*. 240:C80-C89.
3. CALLAWAY, J. C., A. E. STUART, and J. S. EDWARDS. 1989. Immunocytochemical evidence for the presence of histamine and GABA in photoreceptors of the barnacle (*Balanus nubilus*). *Visual Neuroscience*. 3:289-299.
4. CHAN, B. K. K., J. T. HØEG, and R. KADO. 2014. Thoracica, p. 116-124. *In: Atlas of crustacean larvae*. J. W. Margtin, J. Olesen, and J. T. Høeg (eds.). Johns Hopkins University Press, Baltimore.
5. COCHRAN, T. 1968. Effects of predation upon the intertidal cirriped population. Vol. Summer, Book 1. OIMB (ed.), Charleston, OR.

6. CORNWALL, I. E. 1951. Arthropoda: Cirripedia. *In*: Canadian Pacific Fauna. University of Toronto Press for the Fisheries Research Board of Canada, Toronto.
7. —. 1977. The Barnacles of British Columbia. British Colonial Provincial Museum, Victoria.
8. DARWIN, C. 1854. A Monograph of the subclass Cirripedia (Part II Balandiae). Royal Society, London.
9. HENRY, D. P. 1940. The Cirripedia of Puget Sound with a key to the species. University of Washington Publications in Oceanography. 4:1-48.
10. HOYLE, G., and T. SMYTH, JR. 1963. Giant muscle fibers in a barnacle, *Balanus nubilus* (Darwin). *Science*. 139:49-50.
11. HØEG, J. T., P. L. LIIG, R. R. STRATHMANN, and D. S. WETHEY. 1987. Phylum Crustacea, class Maxillopoda, subclass Cirripedia, p. 370-392. *In*: Reproduction and development of marine invertebrates of the northern Pacific coast. M. F. Strathmann (ed.). University of Washington Press, Seattle.
12. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
13. KURIS, A. M., P. S. SADEGHIAN, J. T. CARLTON, and E. CAMPOS. 2007. Decapoda, p. 632-656. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
14. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
15. MORRIS, C., and H. LECAR. 1981. Voltage oscillations in the barnacle giant muscle fiber. *Biophysical Journal*. 35:193-213.
16. NEWMAN, W. A. 2007. Cirripedia, p. 475-484. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley.
17. PALMER, A. R. 1982. Predation and parallel evolution: recurrent parietal plate reduction in Balanomorph barnacles. *Paleobiology*. 8:31-44.
18. PEREZ-LOSADA, M., M. HARP, J. T. HØEG, Y. ACHITUV, D. JONES, H. WATANABE, and K. A. CRANDALL. 2008. The tempo and mode of barnacle evolution. *Molecular Phylogenetics and Evolution*. 46:328-346.
19. PILSBRY, H. A. 1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum; including a monograph of the American species. U.S. National Museum Bulletin. 93:1-366.
20. RICKETTS, E. F., and J. CALVIN. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
21. ROSS, W. N., L. L. STOCKBRIDGE, and N. L. STOCKBRIDGE. 1986. Regional properties of calcium entry in barnacle neurons determined with Arsenazo III and a photodiode array. *Journal of Neuroscience*. 6:1148-1159.
22. STOCKBRIDGE, N., and W. N. ROSS. 1984. Localized Ca²⁺ and calcium activated potassium conductances in terminals of a barnacle photoreceptor. *Nature*. 309:266-268.
23. YONGE, C. M. 1963. The Sea shore. Atheneum, New York.

Updated 2015

Mollusca

Lottia digitalis

A fingered limpet

Phylum: Mollusca
Class: Gastropoda, Prosbranchia
Order: Archeogastropoda, Patellacea
Family: Lottidae

Description

Size—about 25 mm (one inch); largest 30 mm (Haven 1971); average under 15 mm; this specimen 20 mm (Ricketts and Calvin 1971).

Color—greenish gray to dull brown; large solitary animals sometimes more brilliantly marked (Ricketts and Calvin 1971); ribs usually not lighter than spaces between them (Carlton and Roth 1975); always a solid brown spot 'owl-shaped' inside shell on the apex (fig 3); a horseshoe-shaped muscle scar open at the anterior end (fig. 3) (Keen 1971).

Shell Shape—oval, caplike, fairly high elevation (but not all as high as this specimen, fig. 2); apex above or even overhanging anterior margin, forming hook. Strong rough ribs on posterior slope, forming moderately scalloped edge (fig 1), may be absent on anterior slope. Posterior convex, anterior concave (fig 2).

Body—no dark spots on head or sides of foot: species characteristic; a pair of uncini (flap-like structures) on basal plate of radula (inside mouth), a remnant of marginal teeth (Keen 1971): genus *Lottia*. This characteristic observable only by a drying and staining lab preparation (not figured).

Possible Misidentifications

There may be as many as 16 species of rocky intertidal limpets on our coast; few are as adaptable as *L. digitalis* in tolerating different habitats, especially in estuaries. (*L. digitalis* and *L. pelta* are the only limpets that penetrate very far into Coos Bay's estuary).

Lottia pelta, sometimes estuarine, has heavy ribs like *L. digitalis*, but lacks the concave anterior slope of the latter (its anterior slope is convex). Its apex is subcentral, not near the anterior margin; its ribs are usually equally developed on all slopes, and it is smoother than *L. digitalis*. It can have a pattern of radial bands or of white checks. It occurs at lower tidal levels than does *L. digitalis*.

The above limpets of the family Acmaeidae differ from the Patellidae in having only a single ctenidium (feather-shaped gill)

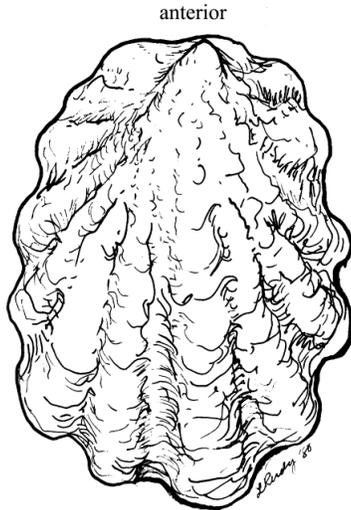
(figure 4). Other genera of Acrriaeldae besides *Lottia*, above, cannot be keyed by shell alone: differences in radula are important as well (Keen 1971). General ways of distinguishing them by shell include the following:

Acmaea sp. have a nearly central apex, the shell is white to pink-rayed, and the radula is adapted for browsing on coralline algae. They are chiefly sublittoral. (The name *Acmaea* once encompassed those limpets now called *Lottia* and *Notoacmea*. These have now been divided: *Lottia* sp. have uncini (marginal teeth) on the radula; they have fine to heavy radial ribs and an apex anterior to the center as well as a convex posterior slope. *Notoacmea* lack the uncini on the margin of the radula; they are not heavily ribbed, the apex can be subcentral to quite anterior.) *Notoacmea persona*, a nocturnal limpet preferring shade and caves as a habitat, has an anterior apex directed anteriorly, and a straight anterior slope; the posterior slope is convex. The surface has fine regular striae, not strong ribs. *N. persona* can be large (53 mm) and is found above *Lottia* in the tidal zone (Fritchman 1961). It is chiefly an inhabitant of the open coast, but has been found in quiet waters in Puget Sound (Kozloff 1974b).

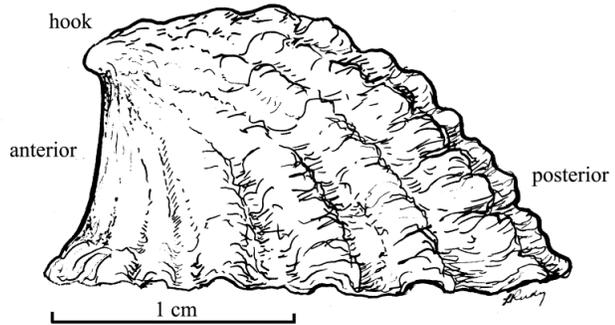
Notoacmea scutum is a thick shelled, rather flat limpet with a subcentral apex, a coarse sculpture of flat ridges (actual radial lines). It is occasionally found in bays (Puget Sound) (Kozloff 1974b).

Two other species of *Lottia* have heavy ribbing, and could be confused with *L. digitalis*; they also inhabit similar territory, at least on the outer coast. The chief inhabitant of the high splash zone is the rough limpet *L. scabra*, with strongly projecting ribs, a strongly scalloped margin, low profile, and both posterior and anterior slope being convex. It has distinctive black spots on its head and on the sides of its foot. It prefers gently sloping or horizontal surfaces. Its range is generally too far south for Oregon.

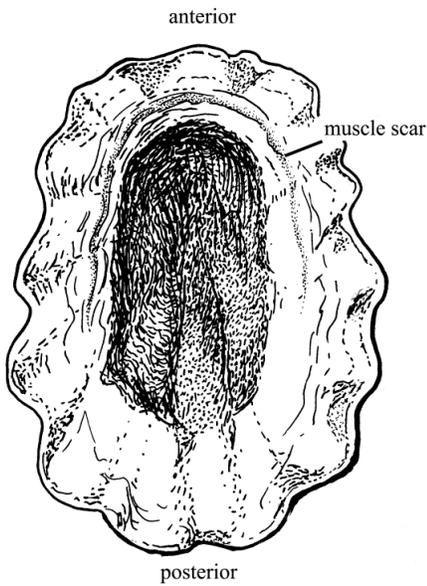
Lottia digitalis



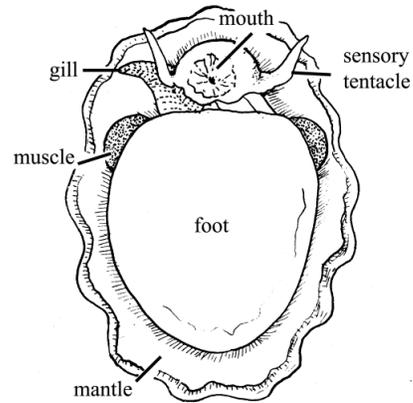
1. *Lottia digitalis* (dorsal view, L:2cm) x4:
strong ribs; scalloped edge; rough surface.



2. (Lateral view) x4:
moderate elevation; apex hook-like, near
anterior end; anterior slope concave; posterior
slope convex.



3. Shell interior x4:
solid brown spot at apex;
horse-shoe shaped muscle
scar.



4. Schematic of animal (ventral view)

L. strigatella, formerly *C. paradigitalis*, was once thought to be a 'hybrid' of *L. digitalis* and *L. pelta* (Carlton and Roth 1975). It is the closest species to *L. digitalis*, but is smoother, has fine radial lines, but no ribs; a convex posterior, slightly concave anterior slope, and is only to 20 mm in length. Its apex is often eroded. The interior is glossy, bluish white with brown stains, and with the outside pattern showing through (Keen 1971). The animal is completely white. This species is found with *L. digitalis* at Coos Head, just inside the bay entrance, under marine conditions (Frank 1965a).

Ecological Information

Range—Unalaska Island south to Guadalupe Island, Baja California.

Local Distribution—outer coast; bays: Coos Bay-Coos Head, lower South Slough.

Habitat—prefers steep slopes in upper (splash) zone (Haven 1971); pilings (in bays); tolerates 'variable and hazardous' conditions (Frank 1965c); mud, swirling sand, debris, industrial pollution, sewage, strong wave action. In lower levels (zone 2 in Ricketts and Calvin 1971) lives among barnacles, algae on flat surfaces. This specimen on a log. Avoids dessication but tolerates and requires aerial conditions (Haven 1971). Found on 'virtually all hard substrates' (Haven 1971).

Salinity—tolerates a wide range, from concentrated sea water to fresh water (Wolcott 1973).

Temperature—a cold water species; tolerates high temperatures less well than does *L. scabra* (Wolcott 1973). Found more commonly in winter than summer (central California) (Haven 1971).

Tidal Level—oldest and largest animals are found highest; found from higher high tides up into splash zone (zone 1 in Ricketts and Calvin 1971); adapted to dessication better than most limpets, and is never found permanently submerged: lower limit: zone 2, at about mean high water (Frank 1965c; Keen 1971).

Associates—in flat areas of zone 2: algae, barnacles, amphipods *Orchestoidea*, *Orchestia*; gribble *Limnoria*, littorine snails, insects (springtails). On vertical rock surfaces, Coos Head: *L. paradigitalis* (*strigatella*), *Balanus glandula*, *Littorina scutulata*, *L. pelta* (at lower limit) (Frank 1965c). On pilings:

Balanus. In California: *L. scabra*, *L. gigantea* (at lower limit) (Haven 1971).

Quantitative Information

Weight—

Abundance—most common upper intertidal limpet in Oregon (Frank 1965c); within its range, common from Monterey north (Ricketts and Calvin 1971). Tends to aggregate (Millard 1968).

Life History Information

Reproduction—separate sexes; eggs and sperm shed into sea; length of planktonic life unknown (Haven 1971). Spawning winter and spring; peak recruitment: spring (Fritchman 1961).

Growth Rate—very consistent (Frank 1965c), fastest fall and winter, stopped in summer; growth decreased by crowding.

Longevity—occasionally 6 years (Frank 1965a).

Food—encrusting microalgae: blue greens, diatoms (Frank 1965c).

Predators—sea stars, oyster catchers; shorebirds, *Pachygrapus* (Morris et al 1980).

Behavior—does not 'home' precisely like *L. scabra*, but has a home range (Haven 1971). Has a seasonal vertical migration: higher in winter (with higher waves). Secretes mucus sheet between itself and substrate to aid in slowing dessication and because it doesn't fit precisely into the rock. Can accumulate large concentrations of lead (*ie.* animals under Golden Gate Bridge) (Morris et al 1980).

Bibliography

1. CARLTON, J. T., and B. ROTH. 1975. Phylum Mollusca: Shelled Gastropods, p. 467-514. *In*: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
2. FRANK, P. W. 1965a. Growth of three species of *Acmaea*. *Veliger*. 7:201-202.
3. ——. 1965c. The biodemography of an intertidal snail population. *Ecology*. 46:831-844.
4. FRITCHMAN, H. K. 1961. A study of the reproductive cycles in the California *Acmaeidae* (Gastropoda). *The Veliger*. 3:57-63, 95-101.

5. HAVEN, S. B. 1971. Niche differences in the intertidal limpets *Acmaea scabra* and *Acmaea digitalis* (Gastropoda) in central California. *The Veliger*. 13:231-248.
6. KEEN, A. M. 1971. Sea shells of tropical west America; marine mollusks from Baja California to Peru. Stanford University Press, Stanford.
7. KOZLOFF, E. N. 1974b. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago. University of Washington Press, Seattle & London.
8. MILLARD, C. P. 1968. The clustering behavior of *Acmaea digitalis*. *The Veliger*. 11 Supplement:45-51.
9. MORRIS, R. H., D. P. ABBOTT, and E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California.
10. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
11. WOLCOTT, T. G. 1973. Physiology, ecology, and interzonation in limpets (*Acmaea*), a critical look at 'limiting factors'. *Biological Bulletin*. 145:389-422.

Updated 1983

Lottia pelta

The shield, or helmet limpet

Phylum: Mollusca
Class: Gastropoda, Prosobranchia
Order: Archeogastropoda, Patellacea
Family: Lottidae

Description

Size—25mm (Brusca and Brusca 1978); can reach 40 mm farther north (Kozloff 1974b); this specimen, 32.5 mm.

Color—extremely variable; called the brown and white shield limpet by Ricketts (Ricketts and Calvin 1971); gray, slightly raised ribs with white between them; some specimens without ribs, but with a checkered or striped pattern. Slightly hooked apex eroded.

Shell Shape—elevated (height usually greater than $\frac{1}{3}$ length (Carlton and Roth 1975); surface with fine regular ribbing, anterior space straight or very slightly concave; apex subcentral, very slightly directed anteriorly (fig 2); posterior slope slightly convex, nearly straight (Kozloff 1974a). Margin slightly scalloped.

Interior—blue gray to white, with subapical brown spot (fig 3), and horseshoe-shaped muscle scar joined by a thin, faint line (fig. 3) (Keen and Coan 1974).

Young—some subadults (over 6 mm) with dark brown exterior, lustrous, smooth and with fine radial sculpture, living on alga *Egregia*. Interior light brown to gray, with postapical brown spot. (*Notoacmaea insessa*, of which subadult *pelta* is so similar, is dark brown inside.)

Possible Misidentifications

Although a very many species of limpets of the family Acmaeidae occur on our coast; only about 4 are found in estuarine conditions. Some of these belong to the genera *Notoacmea*, which like *Lottia* have a horseshoe-shaped muscle scar on the shell interior, joined by a thin curved line; an apex anterior to the center; and various coloration, but not pink-rayed or white. These two genera differ mainly in that *Lottia* has a pair of uncini or teeth on the radula (not figured), while *Notoacmea* does not. Also, *Notoacmea* sp. are usually not heavily ribbed, while *Lottia* species are (Keen 1971).

Lottia digitalis, the common fingered limpet, differs from *L. pelta* in having an apex very close to or even overhanging the anterior

margin, which forms a strong hook; its anterior slope is concave. This species has strong raised ribs and a moderately scalloped edge; its rough ribs may show only on the posterior slope. It occurs higher in the tidal range than does *L. pelta*.

Lottia strigatella, once thought to be a hybrid of *Lottia digitalis* and *L. pelta*, has been found just inside Coos Bay. Like *L. digitalis*, it has a hooked apex near the anterior margin, and a slightly concave anterior slope. It is small, growing only up to 20 mm, and smooth, with fine radial lines but no ribs.

A bay dwelling form of *Lottia limatula*, *L. l. moerchii*, has a higher elevation than the usual form of that species. It has buff and dark mottling, or greenish brown with white bands; its ribs are imbricated (set like tiles); its edges are serrated. It has not been found as far north as Oregon.

Notoacmea scutum, found only occasionally in bays, is thick shelled, rather flat, with a coarse sculptured surface (Brusca and Brusca 1978). It sometimes has radial lines quite like those of *L. pelta*. It has a subcentral apex and a low elevation and is often filmed with algae.

Notoacmea persona is also found in bays. It is large, nocturnal and smooth. It has an anterior hooked apex and is dark brown with white checked edges.

Young *L. pelta* can resemble the limpet *Notcacmea insessa* which lives only on the marine alga *Egregia*. *N. insessa* adults are brown, translucent and smooth. (See young, above).

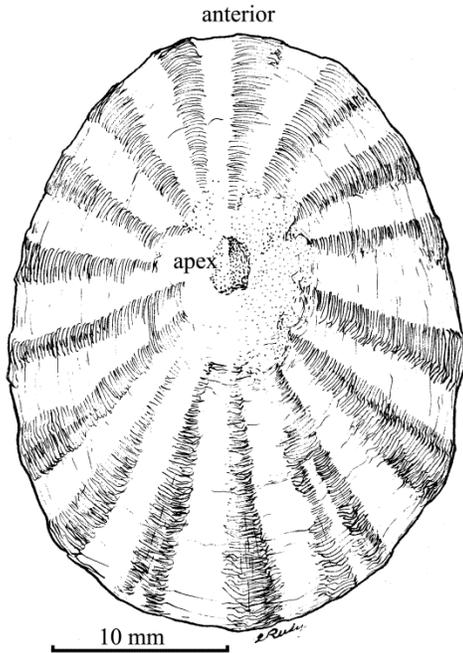
Ecological Information

Range—Aleutian Islands to Punto Santo Tomas, Baja California (Ricketts and Calvin 1971).

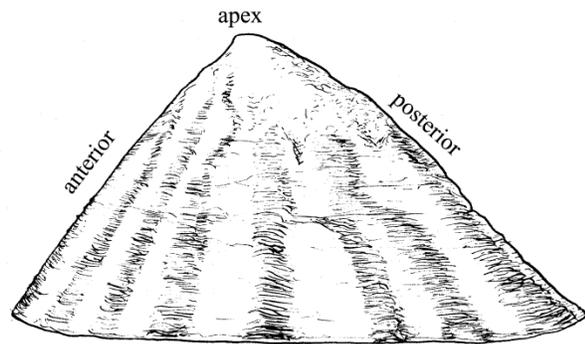
Local Distribution—Coos Bay. South Slough.

Habitat—on rocks (locally), also with various algae in mussel beds (Carlton and Roth 1975); 'eurytopic'; South Slough: on floats, under rocks.

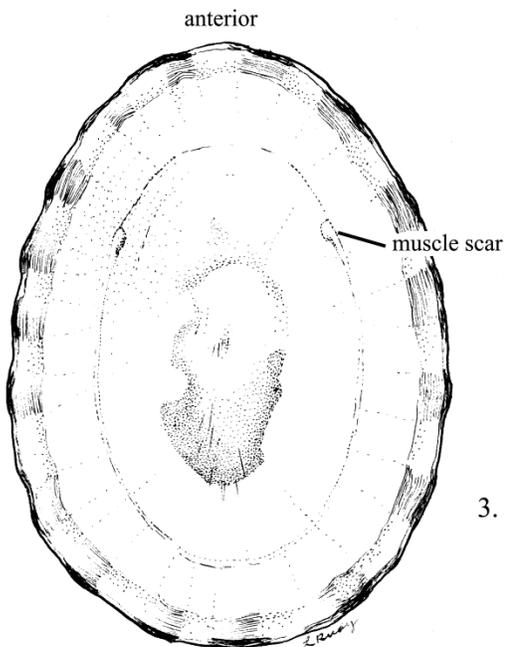
Lottia pelta



1. *Lottia pelta* (L:32.5mm, W:24mm) x3:
uniform gray, low ribs; apex subcentral;
margin slightly scalloped.



2. (Lateral view, H: 17mm) x3:
anterior slope straight, posterior slope
slightly convex; apex subcentral, slightly
hooked.



3. Interior:
horseshoe-shaped muscle scar joined by
thin line; subapical brown spot.

Salinity—collected at 30 ‰ seawater.

Tidal Level—just below *L. digitalis* and *N. persona* (Puget Sound); on rocks usually uncovered by the tide. On outer coast-upper mid- to lower mid-intertidal (Brusca and Brusca 1978).

Associates— *Lottia digitalis*; in mussel/barnacles association on pilings. With algae *Egregia*, *Postelsia Laminaria*, *Endocladia*.

Quantitative Information

Weight—

Abundance—not common in bays; relatively common on outer coast (Brusca and Brusca 1978).

Life History Information

Reproduction—separate sexes; eggs and sperm shed into sea; length of planktonic life unknown (Frank 1965a). Active throughout year; spawns at sea temperatures of 48.5°-60°F (Fritchman 1962).

Growth Rate—probably grow faster than *C. digitalis*, to 30 mm in 3 years (Morris et al 1980).

Longevity—

Food—a grazing herbivore, especially on red and brown algae (Morris et al 1980).

Predators—seastars: *Pisaster ochraceus*, for which it has developed an escape mechanism (Margolin 1964).

Behavior—

Bibliography

1. BRUSCA, G. J., and R. C. BRUSCA. 1978. A naturalist's seashore guide. Mad River Press, Arcata, CA.
2. CARLTON, J. T., and B. ROTH. 1975. Phylum Mollusca: Shelled Gastropods, p. 467-514. *In*: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
3. FRANK, P. W. 1965a. Growth of three species of *Acmaea*. *Veliger*. 7:201-202.
4. FRITCHMAN, H. K. 1962. A study of the reproductive cycles in the California *Acmaeidae* (Gastropoda). *The Veliger*. 4:134-140.
5. KEEN, A. M. 1971. Sea shells of tropical west America; marine

mollusks from Baja California to Peru. Stanford University Press, Stanford.

6. KEEN, A. M., and E. COAN. 1974. Marine Molluscan Genera of Western North America: An Illustrated Key. Stanford University Press, Stanford, California.
7. KOZLOFF, E. N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle & London.
8. ——. 1974b. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago. University of Washington Press, Seattle & London.
9. MARGOLIN, A. S. 1964. A running response of *Acmaea* to seastars. *Ecology*. 45:191-193.
10. MORRIS, R. H., D. P. ABBOTT, and E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California.
11. RICKETTS, E. F., and J. CALVIN. 1971. Between Pacific tides. Stanford University Press, Stanford, California.

Updated 1983

Chlorostoma funebris

The black turban or top shell snail

Phylum: Mollusca
Class: Gastropoda, Prosobranchia
Order: Archeogastropoda
Family: Trochidae

Taxonomy: Check current citations as name is synonymous with *Tegula funebris*.

Description

Size—to 50 mm or more high (Carlton and Roth 1975), usually less than 25 mm (Keep 1935); this specimen 20 mm diameter, 17 mm high.

Color—exterior purplish-black, not shiny; with white eroded apex. Gray when dry. Interior white with a black margin; a pearly or "rainbow" deep interior patch. White around columella (McLean 1969) (fig. 1)

Shell Shape—strong; 4 inflated whorls; rather top-shaped, (conical) with a flat base; round aperture, nearly round, horny operculum: family Trochidae (Griffith 1975). Small snails are about as high as wide (figs. 1, 2); older ones become higher than wide (Frank 1965b).

Sculpture—below the suture is an impressed line (Oldroyd 1924), or a scaly band (Carlton and Roth 1975): "foliaceous incremental lamellae" (Oldroyd 1924) (figs. 1, 2). Whorls "spirally lirated," i.e. having up to 17 thread-like spiral lines (figs. 1, 2); sometimes smooth except for base, or strongly sculptured above (fig. 2).

Umbilicus—covered by a callus, nearly always closed (Carlton and Roth 1975) (fig. 3). Specimens with an open umbilicus do not have a flange between umbilicus and aperture.

Columella—spirally twisted (Oldroyd 1924), with 2 denticles (nodes) near base (fig. 3), lower node worn or indistinct.

Aperture—round, complete; no anterior notch or canal (fig. 3): aperture length less than $\frac{3}{4}$ shell length.

Outer Lip—smooth, black-rimmed, without sculpture (fig. 3).

Operculum—thin; round, numerous spiral lines; horny, not calcareous (fig. 4).

Radula—with a single central tooth; 5-7 pointed lateral teeth, 8-10 marginal teeth (fig. 6).

Foot—long, relatively narrow; with epipodal tentacles along sides: family Trochidae (4 on each side: species *funebris* (fig. 5).

Possible Misidentifications

The Trochidae are herbivorous, conical snails, pearly within, with round, entire apertures and thin horny circular opercula (Griffith 1975). The Turbinidae, a similar family, are also conical, but they have a calcareous operculum, and are represented here only by *Astraea*, a large subtidal and offshore species.

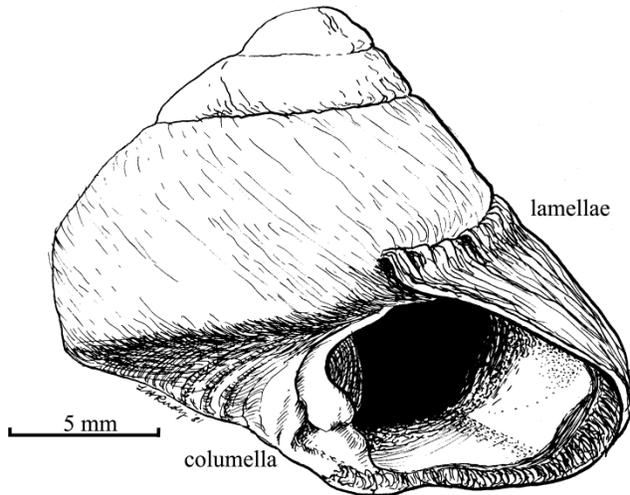
The other common genus of the Trochidae is *Calliostoma*, a conical top shell, which is distinguished from *Chlorostoma* chiefly by its lack of denticles or nodes on the columella. Its whorls are not inflated like *Chlorostoma*'s. *Calliostoma* is found on the outer shores, not in bays; it has many spiral ribs, no umbilicus, and various distinctive colorations.

Snails of the genus *Chlorostoma* have strong columellar nodes, a round, thin, horny operculum with many spiral lines, and a pearly interior. They sometimes have a periostracum. The 3 other species of *Chlorostoma* found on the Pacific coast are not known to be estuarine:

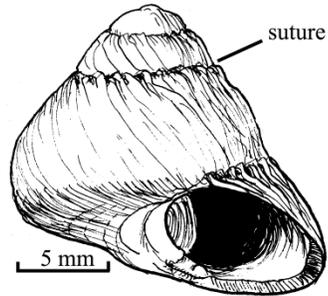
Tegula montereyi probably does not occur above Bolinas Bay, north of San Francisco; it occupies the low intertidal off-shore zone, often in kelp beds. This species is brown, with a strong, open umbilicus and a strictly conical (not inflated) profile.

Tegula pulligo, the dusky turban, occurs in the low intertidal in California; it is the dominant *Tegula* in Puget Sound (Griffith 1975), where it occurs in open coasts and in protected situations (Kozloff 1974a). *T. pulligo* has an open umbilicus with the inner lip produced into a flange (it is closed in *T. funebris*). It has a brown (not purple or black) periostracum; its basic color is brown or gray, sometimes with orange, white or brown spots on the edge. Its habitat is open rocky beaches (Griffith 1975).

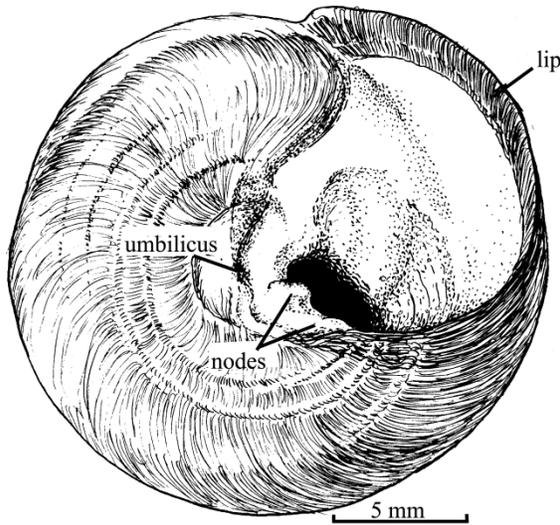
Chlorostoma funebris



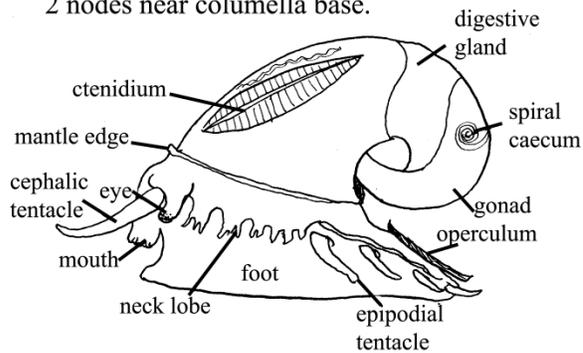
1. *Chlorostoma funebris* (ventral view, H:17mm, D:20mm) x5: four whorls, inflated; eroded spire; elevated lamellae below suture; thread-like spiral sculpture on whorls; base flat.



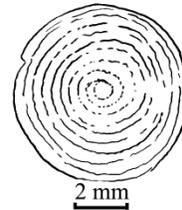
2. Variation x3: strong sculpture on sutures and on whorls.



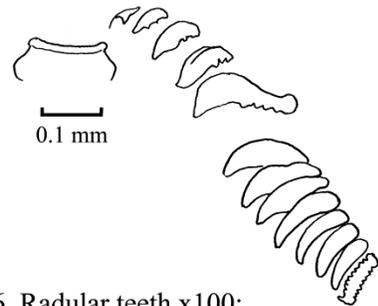
3. (Anterior view) x4.5: aperture rounds, complete; columella white, interior pearly; umbilicus closed; 2 nodes near columella base.



5. Schematic dissection, left side (Abbott et al, 1964).



4. Operculum x4: round, horny, thin; many spiral lines.



6. Radular teeth x100: one large central tooth; 5-7 pointed lateral teeth; 8-10 marginal teeth, last ones serrated (Fritchman, 1965).

Chlorostoma brunnea, the brown turban, is the closest to *C. funebris* in Oregon; it does not seem to occur in Puget Sound (Kozloff 1974a), and is very common on the outer shores in Oregon and around San Francisco (Packard 1918). It has only one node on the columella, as opposed to *C. funebris*' two; its shell is brown or orange brown, and it lacks the scaly subsutural band of *funebris* (Carlton and Roth 1975). *C. brunnea* is found lower in the intertidal than *funebris*, or in off-shore kelp beds near the surface; probably never in estuaries.

Tegula gallina, the speckled tegula, is gray to green, lacks the scaly subsutural band, and is found south of Santa Barbara. It is closely related to *C. funebris*; the radulae are quite similar (Merriman 1967).

Ecological Information

Range—Vancouver, B.C., to central Baja California (McLean 1969).

Local Distribution—marine portions of large Oregon estuaries; Coos Bay: Pigeon Point.

Habitat—avoids exposed outer coast situations although it is found in rocky protected outer tidepools (Carlton and Roth 1975); marine portions of estuaries in rocky situations amongst seaweed (Griffith 1975). Strongly built: can withstand surf. Females found in more exposed places than males at low tide (Frank 1975). Species is negatively phototactic: seeks the light (Morris et al 1980).

Salinity—collected at 30 ‰ salt. Cannot withstand continued exposure to low salinity.

Temperature—found in temperate waters only. With black color can get quite warm during exposure to sun at low tides.

Tidal Level—on outer shores, most common at high inter-tidal (2-0 m) (Frank 1975); found in midintertidal as well. In estuary found at 0-+1 ft. Small snails settle high, live there 5-6 years, then migrate to lower levels (to +0.6- -0.2 m) (Paine 1979).

Associates—on outer coast: slipper shell *Crepidula* and several limpets (*Collisella*), which can be predatory. Empty shells used by hermit crabs.

Quantitative Information

Weight—this specimen 4g wet, with shell.

Abundance—most abundant mid-intertidal grazer (Frank 1975).

Life History Information

Reproduction—dioecious; eggs and sperm exuded into water. Sexes can be determined by color of foot sole: males are light, females darker; female gonad bright green from egg yolk. Egg masses gelatinous, about 3 mm diameter; several hundred eggs, about 0.19 mm diameter. Breeding probably once a year (Paine 1979); reproductive size of snails 14 mm (Paine 1971). Planktonic veliger larvae emerge on 7th day, settle 12th day. Long life of *T. funebris* ensures increased lifetime reproductive effort (Frank 1975).

Longevity—lives up to 30 years; average age may be 10 years (Frank 1975).

Growth Rate—young snails grow rapidly: from 4-5.6 mm and 27 mg average weight (June) to 5.6-9.8 mm. 177.3 mg (following March) (Morris et al 1980). California snails do not show growth rings of Oregon snails, which in older animals reveal an annual winter cessation of growth (Frank 1975).

Food—"a catholic feeder" (Frank 1975): almost any common alga. Prefers *Macrocystis integrifolia*, *Nereocystis luetkeana*, *Rhodoglossum affine*, *Gigartina canaliculata*: i.e. fleshy forms. If not available, will eat encrusting green alga, *Ralfsia pacifica*, detritus (Abbott et al 1964).

Predators—*Pisaster ochraceus* in low intertidal. Although *Chlorostoma* is not its preferred prey, *Pisaster* can consume over ¼ the available snails (Frank 1965b). Possibly limpet *Collisella*; carnivorous snail *Nucella*; crab *Cancer antennarius*.

Behavior—larger animals migrate to lower intertidal. Species is sedentary, aggregates at low tide, moves up to rock tops at nighttime high tides (not diurnal ones) (Morris et al 1980). Territory: tends to live in a radius of about 1.5 m for months; a daily movement of about 1m (Frank 1975). Snails move well on rocks, are clumsy on sand. They place pebbles on the foot to alter balance (Morris et al 1980). Escape predators by sensory perception (seastars), or by crawling onto top of predator's shell (carnivorous snails).

Bibliography

1. ABBOTT, D. P., L. R. BLINKS, J. H. PHILLIPS, and R. H. STOHLER. 1964. The biology of *Tegula funebris*. The Veliger. 6 Supplement.
2. CARLTON, J. T., and B. ROTH. 1975.

- Phylum Mollusca: Shelled Gastropods, p. 467-514. *In*: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
3. FRANK, P. W. 1965b. Shell growth in a natural population of the turban snail *Tegula funebris*. *Growth*. 29:395-403.
 4. ———. 1975. Latitudinal variation in the life history features of *Tegula funebris* (Prosobranchia: Trochidae). *Marine Biology*. 31:181-192.
 5. FRITCHMAN, H. K. 1965. The radulae of *Tegula* species from the west coast of North America and suggested intrageneric relationship. *The Veliger*. 8:11-14.
 6. GRIFFITH, L. M. 1975. The intertidal univalves of British Columbia. British Columbian Provincial Museum Handbook. 26:1-101.
 7. KEEP, J., J. Longstreth (eds). 1935. West coast shells; a description in familiar terms of principal marine, fresh-water, and land mollusks of the United States, British Columbia, and Alaska, found west of the Sierra. Calif., Stanford University Press; London, H. Milford, Oxford University Press, Stanford University.
 8. KOZLOFF, E. N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle & London.
 9. MCLEAN, J. H. 1969. Marine shells of southern California. [Los Angeles] Los Angeles County Museum of Natural History.
 10. MERRIMAN, J. A. 1967. Systematic implications of radular structures of west coast species of *Tegula*. *The Veliger*. 9:399-403.
 11. MORRIS, R. H., D. P. ABBOTT, and E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California.
 12. OLDROYD, I. S. 1924. Marine shells of Puget Sound and vicinity. University of Washington Press, Seattle.
 13. PAINE, R. T. 1971. Energy flow in a natural population of the herbivorous gastropod *Tegula funebris*. *Limnology and Oceanography*. 16:86-98.
 14. ———. 1979. The *Pisaster-Tegula* interaction: Prey patches, predator food preference and intertidal community structure. *Ecology*. 50:950-961.
- Updated 1983

Lithoglyphus virens

Giant Columbia River spire shell

Phylum: Mollusca
Class: Gastropoda
Order: Neotaenioglossa
Family: Hydrobiidae

Description

Size—to 11mm long (Clarke 1981); illustrated specimen (Columbia River) 7.5 mm.

Color—"virens" = green; periostracum chestnut brown to yellowish brown or olive green. With or without dark collabral or spiral bands (Clarke 1981) (this specimen without, fig. 1). Interior white.

Shell Shape—thick, solid, ovate, imperforate; 4 to 5 inflated whorls, nuclear whorl flatly coiled, then decurrent (turning down).

Early coils often corroded (fig. 1); following whorls enlarge rapidly, are convex and separated by deep sutures. Body whorl large and constitutes most of shell (fig. 1).

Sculpture—coarse growth rests, fine collabral lines, obscure spiral striation (fig. 1).

Aperture—subcircular; rounded below, acute above. Simple lip; thickened peristome reflexed over columella region, obscuring umbilicus (fig. 1); sometimes exposing a tiny slit (Clarke 1981) (not in this specimen).

Operculum—thin, pale brown; almost transparent in this specimen (fig. 3); corneous, paucispiral (only three turns) (Clarke 1981). Strong radial wrinkles, fine spiral lines.

Radula—with 7 teeth (2-1-1-2), each with many cusps (Clarke 1981) (not shown).

Animal—tentacles long, cylindrical; gills internal; male with external winged verge behind right tentacle (Clarke 1981) (not shown).

Eggs—round or oval, attached singly to stones or vegetation; family Hydrobiidae (Clarke 1981) (eggs not shown).

Possible Misidentifications

Lithoglyphus spp., known until recently as *Fluminicola*, doesn't seem to have any close relative or obviously similar associates. Its family, the Hydrobiidae, or spire shells, is worldwide, and may be marine, brackish or freshwater (Clarke 1981). The genus has formerly been placed in the family Amnicolidae (as *Fluminicola* (Henderson

1929)), and also in Bulimidae (also as *Fluminicola* (Ward and Whipple 1966)). The present family designation is by Taylor 1966. One species of the genus, (*Fluminicola*) *seminalis*, is found far inland, in the Steens Mountain and Klamath Falls areas of Oregon (Henderson 1929). Another, *F. nuttalliana* Lea, now considered a species synonym (Clarke 1981), was formerly differentiated because of its more cylindrical, less inflated shape (Henderson 1929). *L. columbiana* Hemphill (Pilsbry, 1899) is a dark species, once found in the Columbia River to its mouth, and now only at Hanford, in a last bit of free-flowing river. It was listed as an endangered species in 1976 (Clarke 1976). *Lithoglyphus hindsii* (Baird, 1863) is also a synonym for *L. virens*, being simply an older name (Clarke 1981).

Ecological Information

Range—Idaho, Wyoming, Utah, Washington and Oregon. Kootenay, Wigwam and Columbia Rivers of British Columbia (Clarke 1981).

Local Distribution—Columbia, Siuslaw Rivers (Clarke 1981); N. Umpqua at Winchester Bay; mouth of Deschutes River; Yaquina River at Eddyville; Santiam River (Henderson 1929).

Habitat—on and under rocks and among vegetation in large and medium lakes, rivers, creeks; in rapid to slow currents (Clarke 1981).

Salinity—considered a freshwater species, it is found in lower reaches of Oregon's rivers.

Temperature—

Tidal Level—

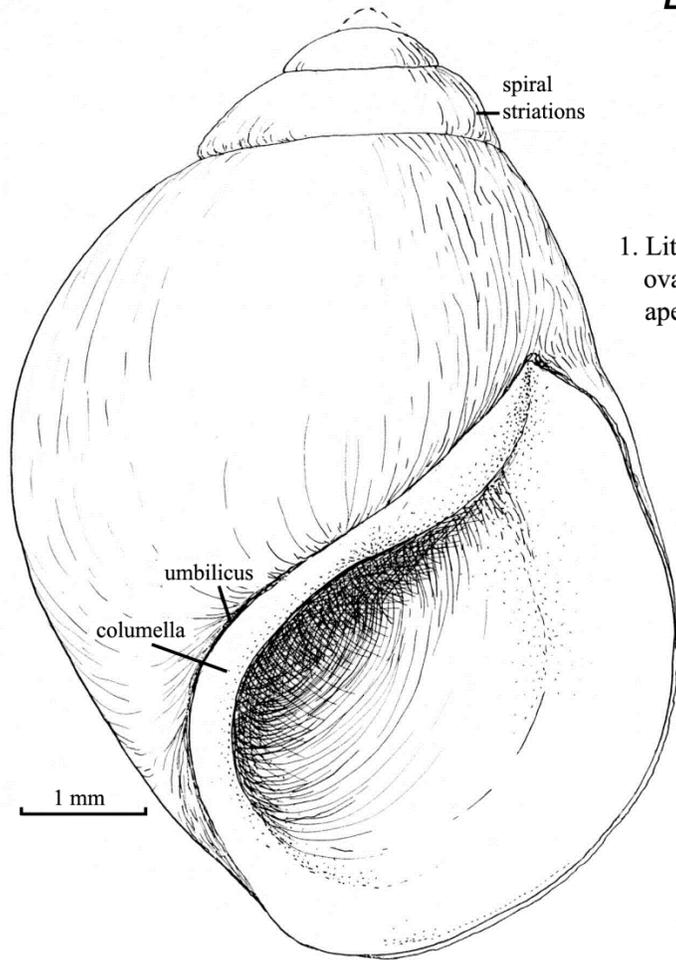
Associates—

Quantitative Information

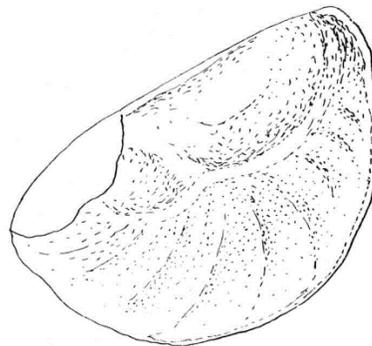
Weight—

Abundance—

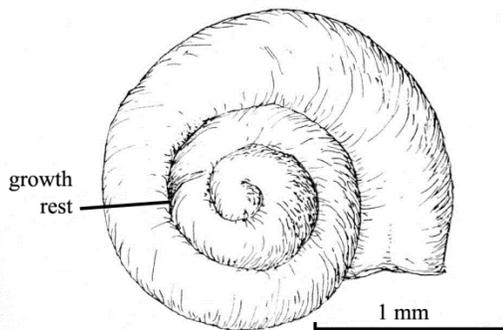
Lithoglyphus virens



1. *Lithoglyphus virens* (L:7.5mm) x20:
ovate, smooth; large body whorl;
aperture subcircular, lip simple.



3. Operculum x30:
(from small specimen, 4.2 mm)
thin, pale, transparent;
few spirals; radial wrinkles.



2. Dorsal view x30
(small specimen, 2.5 mm).

Life History Information

Reproduction—dioecious (separate sexes); lays eggs which are attached singly to stones or to vegetation (Clarke 1981).

Growth Rate—

Longevity—

Food—

Predators—

Behavior—

Bibliography

1. CLARKE, A. H. 1976. Endangered freshwater mollusks of northwestern North America. Bulletin of the American Malacological Union. 43:18-19.
2. ——. 1981. The freshwater molluscs of Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Canada.
3. HENDERSON, J. 1929. Non-marine Mollusca of Oregon and Washington. [University of Colorado], Boulder, Colo.
4. TAYLOR, D. W. 1966. Summary of North American Blancon nonmarine mollusks. Malacologia. 4:1-172.
5. WARD, H. B., and G. C. WHIPPLE. 1963. Fresh-Water Biology. John Wiley & Sons; New York.

Updated 1988

Assiminea californica

A small salt marsh snail

Phylum: Mollusca
Class: Gastropoda, Prosobranchia
Order: Mesogastropoda
Family: Assimineidae

Description

Size—less than 4 mm high; most specimens collected near 3 mm.

Color—glossy chestnut (Keen 1971), smooth, transparent (largest whorl); interior porcelain-like, not pearly; spire often almost black (Coos Bay specimens); animal white with black markings (fig. 4).

Shell Shape—5 whorls: rounded, convex; globose to turbanate (Keen and Coan 1974), taller than wide; aperture subcircular, without notch or canal; inner lip spread out as a small thickened callus (Keen and Coan 1974) (fig. 3).

Columella—continuous with inner lip: no shelf, no folds, appressed to whorl. Spreads into callus. (fig. 3).

Animal—eyes on short ocular peduncles, no tentacles: family Assimineidae (Keen 1971) (fig. 4). Radula with 3 basal cusps on both sides of central plate: genus *Assiminea* (not figured).

Operculum—very thin, transparent, subspiral, convex (fig. 2).

Possible Misidentifications

Assiminea californica is one of a small association of salt marsh snails. Within our range it is often found with or near *Littorina (Algamorda) newcombiana*. This is a slightly larger littorine (to 6 mm) with 4 whorls, a nearly circular aperture, and with a simple chink between the large whorl and inner lip. The general shape and appearance of the two gastropods is quite similar. *L. (A.) newcombiana* does not have ocular peduncles.

A 2nd snail common found in salt marshes is *Ovatella myosotis*, a pulmonate of rather olive shape, up to 8 mm long. It is subcylindrical, not turbanate, with a short spire, three columellar folds, and no operculum. (See plate)

Littorine snails are larger than *Assiminea*, but can be superficially similar: *Littorina sitkana*, often found in this association, is globose, almost as wide as long, and has either heavy striated sculpture or dark

horizontal lines. The animal has long tentacles, not *Assiminea*'s unusual ocular peduncles. *Littorina scutulata*, the checkered littorine, is occasionally found in the saltier parts of marshes. It is quite a bit larger than all the preceding snails, and is patterned on its exterior and purple inside.

Ecological Information

Range—Vancouver Island, British Columbia, to Cabo San Lucas, Baja California (Keen 1971).

Local Distribution—Coos Bay, many stations: South Slough, Haynes Inlet.

Habitat—under driftwood, debris, *Salicornia*, in mud.

Salinity—generally a wide toleration of salinities: to 2.4 ‰ seawater; possibly to 16 ‰ (Matthews 1979).

Temperature—varied (salt marsh temperatures).

Tidal Level—family Assimineidae are intertidal⁴; all live above the low tide level; this species likes upper, usually dry parts of the marsh, about 3-4 feet (South Slough, Coos Bay).

Associates—littorines *L. sitkana*, *L. (A.) newcombiana*, pulmonate *Ovatella myosotis*, amphipod *Traskorchestia traskiana*; plants: *Salicornia*, *Distichilis*, *Fucus*.

Quantitative Information

Weight—

Abundance—common in *Salicornia* marshes (Smith and Carlton 1975).

Life History Information

Reproduction—

Growth Rate—

Longevity—

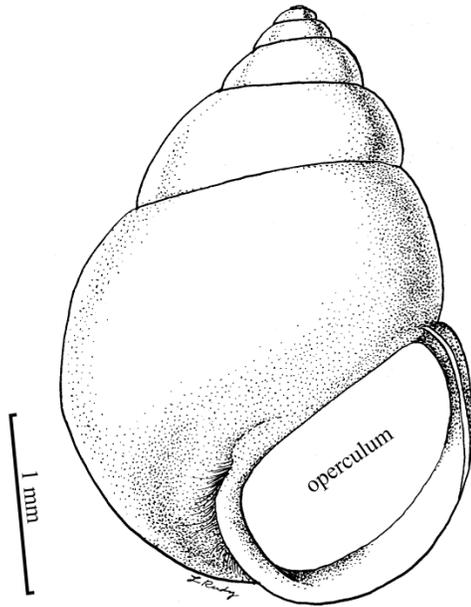
Food—

Predators—fish: many snails found in gut content analysis (Coos Bay) (Matthews 1979).

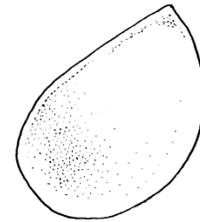
Bibliography

1. KEEN, A. M. 1971. Sea shells of

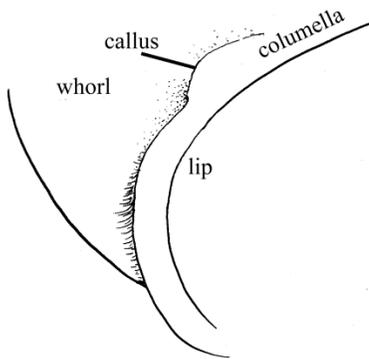
Assimineea californica



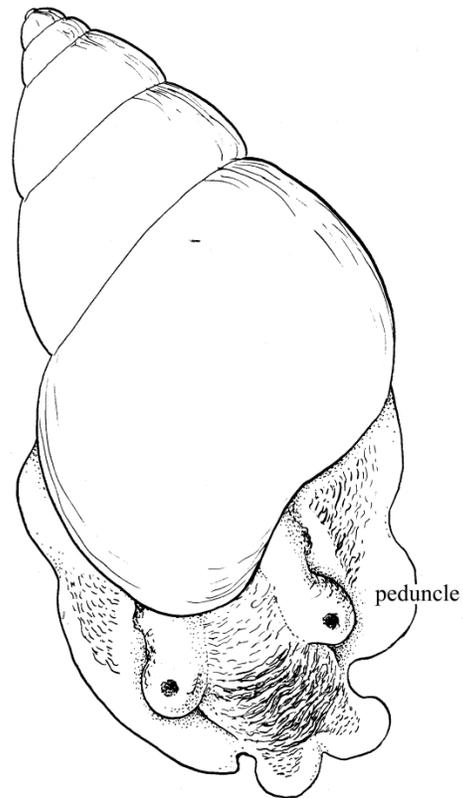
1. *Assimineea californica*
(anterior view, H:3.3 mm) x30:
5 convex whorls, taller than wide.



2. Operculum x30



3. Inner lip x50:
columella continuous with lip,
with no shelf, and a thick callus,
lip appressed to whorl.



4. Animal (dorsal view) x30:
note eyes on ocular peduncles; no tentacles.

- tropical west America; marine mollusks from Baja California to Peru. Stanford University Press, Stanford.
2. KEEN, A. M., and E. COAN. 1974. Marine Molluscan Genera of Western North America: An Illustrated Key. Stanford University Press, Stanford, California.
 3. MATTHEWS, R. 1979. A comparative study of preferred salinities among South Slough snails. Oregon Institute of Marine Biology (University of Oregon).

Updated 1983

Lacuna porrecta

The wide chink shell

Phylum: Mollusca
Class: Gastropoda
Order: Mesogastropoda
Family: Lacunidae

Description

Size—2-4 mm high; $\frac{1}{4}$ to $\frac{1}{2}$ size of *Littorina*.

Color—white to golden brown, with some spiral marking; surface wrinkled, with fine, wavy spiral striae (figs. 1, 4). No white band on inside of aperture, no carina (keel) on largest whorl.

Shell Shape—broad, compact, globose, only 3 whorls (fig 1); shell thin, outer lip 'effuse' (extended); aperture semi-lunar.

Umbilicus—chink is large, with a sharp ridge (fig 3); this groove between whorl and columella is an important key character of the genus *Lacuna*.

Columella—flattened (fig 4): genus *Lacuna*.

Operculum—'paucispiral'; flattened on one side (fig 2).

Animal—*Lacuna* species have metapodial tentacles, which *Littorina* lack (fig 5).

Possible Misidentifications

Adult Lacunidae can be differentiated from Littorinidae by their much smaller size, metapodial tentacles, and chiefly by their umbilical fissure or chink which Littorinidae lack. (Littorinidae have a columella flush with the large whorl). *Lacuna* are often found in eelgrass; *Littorina* almost never are.

There are several species of *Lacuna* on the Pacific coast:

Lacuna unifasciata is more turbate than globose, and has a sharp carina or keel around its largest whorl. It is a southern species, its northern boundary being probably at Monterey Bay, California (Carlton and Roth 1975).

Two Puget Sound species have been identified. Both are larger than our Oregon species: *Lacuna vineta* (= *carinata*, = *solidula*) (Carlton and Roth 1975), is large, about 10 mm long, with 3-4 strong, smooth whorls, a small umbilicus, a white columella, and a strong carina on the last whorl. *Lacuna variegata* is a tall, high-spined form, up to 6 mm high, found in eelgrass (*Zostera*); not described in California keys (Ricketts and Calvin 1971). *L. variegata* has a spreading

outer lip, a wide chink, and zig zag markings (Keep 1935).

The species most like *L. porrecta* and often found with it is *Lacuna marmorata*, the marbled chink shell, usually brown and white, but with a carina on the large whorl, a narrow columellar groove, and often with a white stripe inside the base of the aperture (Carlton and Roth 1975). It has been found in Coos Bay (Keen et al 1942), and hybridizes with other *Lacuna* spp., (Friday Harbor) (Morris et al 1980).

Ecological Information

Range—Bering Sea to San Diego, California (Packard 1918).

Local Distribution—Coos Bay, several stations: South Slough (Keen and Doty 1942).

Habitat—in algae, eelgrass (*Zostera*), or around its roots; in tidepool algae at lower littorine level (Keen et al 1942).

Salinity—

Temperature—genus *Lacuna* essentially a cold water form; few tropical species.

Tidal Level—mid- and low intertidal levels and subtidally; never in upper reaches (Kozloff 1974b).

Associates—hermit crabs, amphipods, littorine snails; encrusted with bryozoans.

Quantitative Information

Weight—

Abundance—not common.

Life History Information

Reproduction—*Lacuna variegata* has eggs like life preservers: yellow, about 5 mm diameter (Kozloff 1974b).

Food—family is herbivorous.

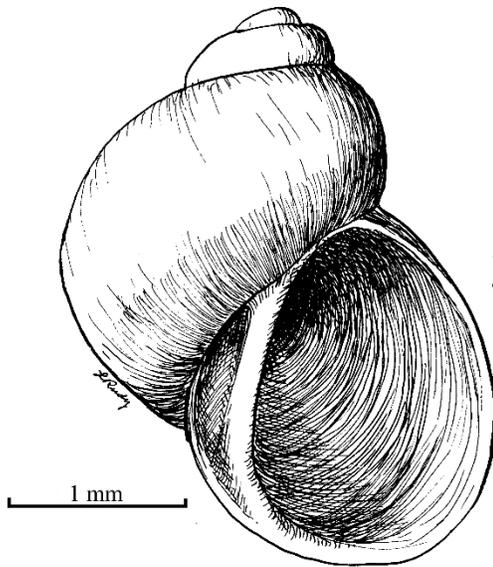
Predators—in eelgrass: seastar *Lepasterias*. Few fishes eat *Lacuna* (Morris et al 1980).

Behavior—it waddles as it moves one side of foot, then the other.

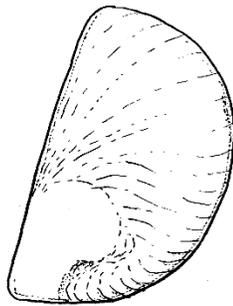
Bibliography

1. CARLTON, J. T., and B. ROTH. 1975. Phylum Mollusca: Shelled Gastropods,

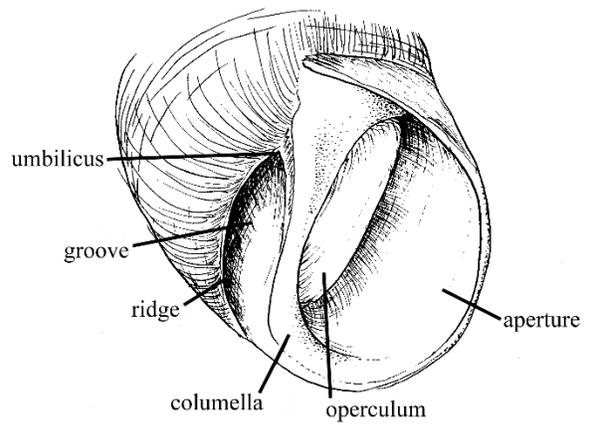
Lacuna porrecta



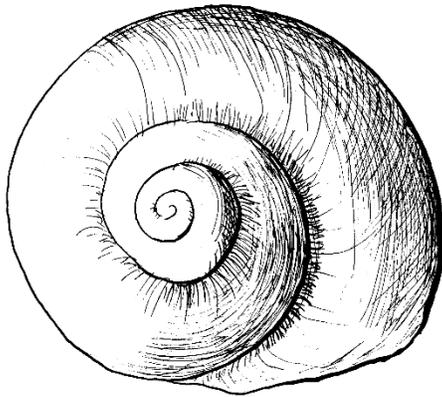
1. *Lacuna porrecta* (anterior view, H:4mm, W:3mm) x30:
3-whorled, thin, globose shell with fine, wrinkled striae;
chink between whorl and columella; outer lip extended.



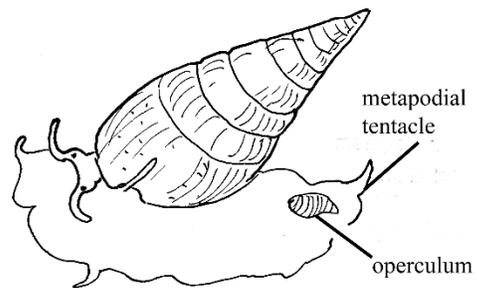
2. Operculum x30



3. Close-up of shell aperture:
umbilicus with sharp ridge, large
groove; flattened columella.



4. (dorsal view).



5. *Nassarius* with metapodial tentacle
(redrawn from Hyman 1967, Adams 1858).

- p. 467-514. *In*: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
2. KEEN, A. M., E. COAN, and C. L. DOTY. 1942. An annotated check list of the gastropods of Cape Arago, Oregon. *Studies in Zoology*. 13.
 3. KEEP, J. and J. Longstreth (eds). 1935. West coast shells; a description in familiar terms of principal marine, fresh-water, and land mollusks of the United States, British Columbia, and Alaska, found west of the Sierra. Calif., Stanford University Press; London, H. Milford, Oxford University Press, Stanford University.
 4. KOZLOFF, E. N. 1974b. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago. University of Washington Press, Seattle & London.
 5. MORRIS, R. H., D. P. ABBOTT, and E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California.
 6. PACKARD, E. L. 1918. Molluscan fauna from San Francisco Bay. 14:199-452.
 7. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.

Updated 1983

Littorina plena

The fine-checked periwinkle

Phylum: Mollusca
Class: Gastropoda
Order: Littorinomorpha
Family: Littorinidae

Taxonomy: Although originally described as separate species by Gould in 1849, *Littorina scutulata* (see description in this guide) and *Littorina plena* were synonymized in 1864 and only became recognized as two separate species again in 1979 (Murray). Illustrations in this guide utilize the same figures for both, *L. plena* and *L. scutulata*. Readers should refer to supplemental materials on our website to differentiate the two species (e.g., photos of shell shading and penis shape).

Description

Size: *Littorina plena* is smaller than the morphologically similar congener, *L. scutulata*, and has an average height of ~9 mm and rarely exceeds 11 mm (Reid 1996); the illustrated specimen (from Coos Bay) is 9 mm in length (Fig. 1). At settlement, individuals are ~ 350 µm.

Color: Color and patterns can be variable but shell exterior is most commonly checkered, and can include a range of colors including dark brown, purple, green, black and white. Other possible patterns include splotches, zig-zags, fine vertical and/or horizontal etched banding, or various combinations of these. Shells are never with strong spiral shape and the exterior sculpture is often encrusted with algae depending on the local habitat (e.g., protected shore vs. wave-exposed shore). The interior of the shell is nearly always purple (Keep and Longstreth 1935).

General Morphology: Shelled gastropods can crawl and burrow using a muscular **foot** and have a head with **eyes** and **tentacles**, a mantle (which secretes the **shell**) and a **radula** that is composed of many teeth for tearing and rasping algae. Gastropods are characterized by torsion, where the body rotates early in development such that the

visceral mass (e.g. anus, mantle cavity) is directly above the foot (rather than posterior to) (McLean 2007). The Littorinidae are small-shelled snails with a rounded peristome (Plate 378, Reid 2007). Two local species in the family Littorinidae, *Littorina scutulata* and *L. plena*, are morphologically very similar and require examination of penis morphology for differentiation (Fig. B2, supplemental images on our website and **Possible Misidentifications** in this text).

Shell: The checkered shell pattern of *L. plena* is composed of smaller checks than *L. scutulata*. They are usually black/dark brown and white. Individuals exhibit a range of shell patterns and colors including a solid purple/black (Reid 1996). Other reported differences include the presence of a basal ridge and a distinct light-colored basal band in the body whorl of *L. scutulata* which is absent in *L. plena* (Rugh 1997; Hohenlohe and Boulding 2001). Shells should be wet to fully examine colors and patterns.

Shape: The overall shell shape is conical, with four whorls, and lacking a columellar groove (inner lip) or chink. Shell shape is known to vary depending on local conditions and snails on wave-exposed shores have shorter, thinner shells with a larger aperture (allows a larger foot to help prevent dislodgment) whereas snails on protected shores have larger, thicker shells with a smaller aperture, which may reduce predation by crabs (Rugh 1997)

Interior: *Littorina* spp. lack posterior or metapodial tentacles, having only cephalic tentacles (Carlton and Roth 1975) (see dissection, Fig. A3).

Exterior:

Aperture:

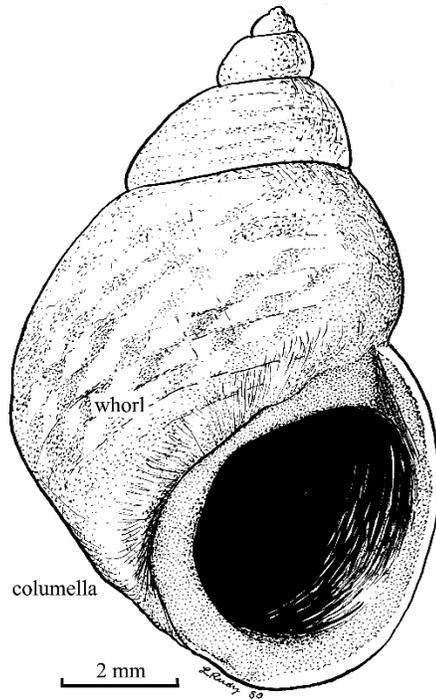
Inner (Columella) and Outer Lip:

Umbilicus:

Tentacles: *Littorina plena* tentacles typically have a mostly-unbroken longitudinal stripe

Figure A

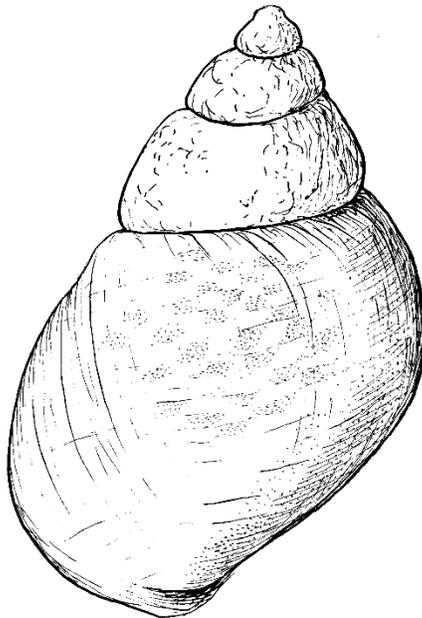
Littorina scutulata and *plena*



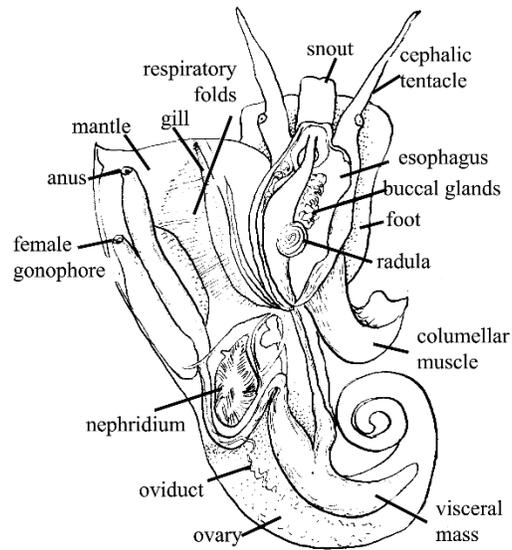
1. *Littorina scutulata* and *plena* (anterior view, H: 9mm) x12: conical, four whorls; no columellar groove; surface checkered, interior purple.



1a. Operculum.

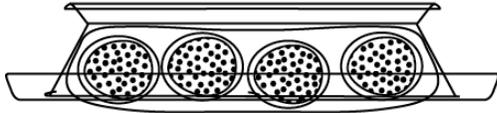


2. (Posterior view) x12.

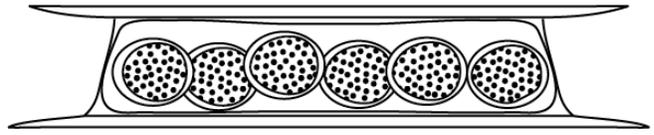


3. Dissection of female *Littorina* sp.: mantle cut, turned over (Hyman, 1967; Souleyet, 1852).

Littorina scutulata and *plena*



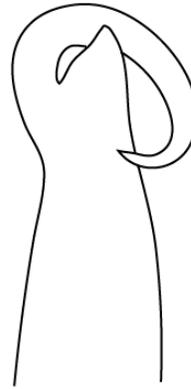
1a. *L. scutulata* egg case.



1b. *L. plena* egg case.



2a. *L. scutulata* penis.



2b. *L. plena* penis.



3a. *L. scutulata* tentacle.



3b. *L. plena* tentacle.

Illustration by Jenna Valley

with or without transverse bands, but they can also be all-dark (Fig. B3).

Eyes:

Siphons:

Foot:

Operculum: Solid, horny, and brown operculum with spiral lines originating in the bottom half (Fig. A1a).

Radula:

Possible Misidentifications

Snails in the genus *Littorina* (family Littorinidae) are very common members of the intertidal, however their similarity in shell morphology renders species difficult to differentiate. Species level identification requires examination of the penis and pallial oviduct (Reid 1996, 2007). A similar but smaller genus of another family is *Lacuna*, the small 'chink' shell, which has a groove, or chink, between the large whorl and the columella. *Littorina* lacks this groove. The Lacunidae are often found in eelgrass, (*Littorina* is not), and are never in the upper intertidal area, as *Littorina* often is (Kozloff 1974a).

There are seven species in the genus *Littorina* locally. Of those species, at least three also have the solid shell and absence of columellar groove found in *L. plena*. *Littorina planaxis* is an inhabitant of the outer shore intertidal although individuals are also found in Puget Sound, Washington and, occasionally in more marine parts of Oregon's estuaries. It is stout and globose, and usually larger than *L. scutulata* (Brusca and Brusca 1978), with a broad, flat, polished columella (Keep and Longstreth 1935). *Littorina planaxis* is essentially a southern form, although it does occur occasionally in Puget Sound (Kozloff 1974a), and its niche is generally taken over northwards at about Cape Arago, Oregon, by *L. sitkana* (Ricketts and Calvin 1971). *Littorina sitkana* is a fat, globose littorine, with rounded columella, and strong spiral ridges on its whorls. It can be white to black, but is often a yellowish brown (Keep and Longstreth 1935). A smaller variety was formerly called *L. rudis*. This species can be strongly striped, or rough and striated. It is fairly common in salt marshes, and can be up to 15 mm tall (Kozloff 1974a).

Littorina (Algamorda)

newcombiana (= *subrotundata*) is a small, rare salt marsh littorine originally thought to be a freshwater snail. It is light colored, with four rounded whorls, and usually striped. The shell is smooth, thin and covered with a brown periostracum and the aperture is almost circular. It is only about 5 mm long, and has a simple gap, (not a groove) between the whorl and the columella (Keen and Coan 1974). It is found quite high in the intertidal area of the marsh.

Littorina littorea, is an Atlantic species that was introduced into California bays 100 years ago. It is quite thick-shelled, globose and brown to black, with fine dark spiral bands (Abbott 1968). It has not yet been reported in Oregon (Carlton and Roth 1975).

Ecological Information

Range: Type locality is San Francisco, California (Mastro et al. 1982), with known range from Sitka, Alaska to Cabo San Lucas, Baja California.

Local Distribution: Local distribution in outer coast and bays including Coos Bay, South Slough, and the Siuslaw River, near Florence (Matthews 1979).

Habitat: Snails are often found on rocks and pilings on both the rocky outer coast and protected shores. *Littorina plena* is most abundant on sheltered shores and can often be found in salt marshes (Reid 1996), but rarely found in eelgrass (Kozloff 1974a). Individuals are very tolerant of near-terrestrial conditions (Brusca and Brusca 1978).

Salinity: Individuals are found near full sea water (e.g., salinities of 30) on the open coast, as well as in conditions of somewhat reduced salinity (Carlton and Roth 1975). This species does not penetrate upper (and fresher) parts of estuary (Coos Bay). The salinity tolerance ranges from 22–24 (Brusca and Brusca 1978).

Temperature: Occurs over a wide range.

Tidal Level: Individuals are not found more than a few feet above high tide line but are found at higher levels in salt marshes (Kozloff 1974b). *Littorina* spp. are "just above the reach of the waves, along the shores of the entire bay" (San Francisco, California, Packard 1918).

Associates:

Abundance: Individuals are relatively common in rocky areas (Brusca and Brusca 1978). *Littorina plena* and *L. scutulata* are probably the most common littorine in bays, as well, at least in more open coastal habitats.

Life-History Information

Reproduction: Dioecious (separate sexes) with internal fertilization. Most copulation occurs in spring and summer, *en masse*, with a spawning season of April to early October. Sexual maturity occurs when shells are ~2–3 mm in height (by 1 year of age) and they produce negatively-buoyant pelagic egg cases, the morphology of which can be a reliable species indicator (Fig. B1 and supplemental images on our website). At 12–14°C, *L. plena* veligers hatch after 8 days with an initial size of ~135 µm. The planktonic period of the planktotrophic veligers can last 4+ weeks, although competency to settle can be reached by 3 weeks (Hohenlohe 2002). Egg capsules contain pink embryos (although other colors in different regions have been reported (Buckland-Nicks and Chia 1973) and random color variations within a region are sometimes encountered. *Littorina plena* egg capsules are large (~1,100 µm in diameter), with near-equal flat rims (smaller rim is >90% the diameter of the larger rim), and generally have ~6–47 embryos (considerably more than *L. scutulata*, see description in this guide). A third egg capsule is also produced and exhibits a morphology with only one rim. The number of embryos per capsule may vary geographically (Hohenlohe 2002). The penis can be observed by grasping the spire of a submerged snail positioned aperture-up, providing a surface for the snail to grab onto (e.g., probe), and gently pulling away. The penis is orange-pink in color and is attached just behind the base of the right tentacle. The penis in *L. plena* exhibits a bifurcation that occurs further from the tip resulting in a long and often-coiled projection (see supplemental images on our website). The pallial oviduct in females is also distinctive but requires removal of the shell to be seen.

Larva:

Juvenile:

Longevity: The lifespan of the congener, *L. scutulata*, is estimated to be at least 7 years (Behrens 1974). The longevity of *L. plena* is not known.

Growth Rate:

Food: Herbivorous. Littorines rasp microscopic (e.g., *Endocladia*, unicellular green and blue green algae, diatoms), and macroscopic algae (e.g., *Cladophora*, *Pelvetia*, *Rhodoglossum*) from rocks (Castenholz 1961; Dahl 1964).

Predators: Crabs, fish, birds, and predatory gastropods.

Behavior: Individuals live in a “home territory”, i.e., they stay in a small area near a certain pool and “emerge by night, and submerge by day” (Abbott and Haderlie 1980). Snails are generally active when submerged and are often found clustered in groups and/or in crevices during low tide.

Bibliography

1. ABBOTT, D. P., and E. C. HADERLIE. 1980. Prosobranchia: marine snails. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
2. ABBOTT, R. T. 1968. Seashells of North America; a guide to field identification. Golden Press, New York.
3. BRUSCA, G. J., and R. C. BRUSCA. 1978. A naturalist's seashore guide. Mad River Press, Arcata, CA.
4. BUCKLAND, J., F. S. CHIA, and S. BEHRENS. 1973. Oviposition and development of two intertidal snails, *Littorina sitkana* and *Littorina scutulata*. *Canadian Journal of Zoology*. 51:359-365.
5. CARLTON, J. T., and B. ROTH. 1975. Phylum mollusca: shelled gastropods, p. 467-514. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
6. CASTENHOLZ, R. W. 1961. The effect of grazing on marine littoral diatom populations. *Ecology*. 42:783-794.
7. DAHL, A. L. 1964. Macroscopic algal foods of *Littorina planaxis* Philippi and *Littorina scutulata* Gould. *The Veliger*. 7:139-143.

8. HOHENLOHE, P. A. 2002. Life history of *Littorina scutulata* and *L. plena*, sibling gastropod species with planktotrophic larvae. *Invertebrate Biology*. 121:25-37.
9. HOHENLOHE, P. A., and E. G. BOULDING. 2001. A molecular assay identifies morphological characters useful for distinguishing the sibling species *Littorina scutulata* and *L. plena*. *Journal of Shellfish Research*. 20:453-457.
10. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
11. KOZLOFF, E. N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
12. —. 1974b. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago and adjacent Regions. University of Washington Press, Seattle and London.
13. MASTRO, E., V. CHOW, and D. HEDGECOCK. 1982. *Littorina scutulata* and *Littorina plena*: sibling species of two prosobranch gastropod species conformed by electrophoresis. *Veliger*. 24:239-246.
14. MATTHEWS, R. 1979a. A comparative study of preferred salinities among South Slough snails, p. 8. Oregon Institute of Marine Biology.
15. —. 1979b. A comparative study of preferred salinities among South Slough snails, p. Book: 2.
16. —. 1979c. A comparative study of preferred salinities among South Slough snails, p. Book: 2. Vol. Fall.
17. MCLEAN, J. H. 2007. Gastropoda, p. 713-739. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
18. —. 2017. Gastropoda, p. 713-753. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
19. MURRAY, T. 1979. EVIDENCE FOR AN ADDITIONAL LITTORINA SPECIES AND A SUMMARY OF THE REPRODUCTIVE-BIOLOGY OF LITTORINA FROM CALIFORNIA. *Veliger*. 21:469-474.
20. PACKARD, E. L. 1918. Molluscan fauna from San Francisco Bay. *Zoology*. 14:199-452.
21. REID. 2007. *Littorina*, p. 761-766. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
22. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
23. RUGH, N. S. 1997. Differences in shell morphology between the sibling species *Littorina scutulata* and *Littorina plena* (Gastropoda: Prosobranchia). *Veliger*. 40:350-357.

Updated 2016
J. Valley and T.C. Hiebert

Littorina scutulata

The checkered periwinkle

Phylum: Mollusca
Class: Gastropoda
Order: Littorinomorpha
Family: Littorinidae

Taxonomy: Although originally described as separate species by Gould in 1849, *Littorina scutulata* and *Littorina plena* were synonymized in 1864 and only became recognized as two separate species again in 1979 (Murray). Illustrations in this guide utilize the same figures for both *L. scutulata* and *L. plena*.

Description

Size: *Littorina scutulata* is generally larger than its morphologically similar congener, *L. plena*, with average height ~11.5 mm. Individuals can reach a shell size up to 17 mm; this specimen (from Coos Bay) is 9 mm in length (Fig. A1). At settlement, individuals are ~ 350 µm.

Color: Color and patterns can be variable but shell exterior is most commonly checkered, and can cover a range of colors including dark brown, purple, green, black and white. Other possible patterns include splotches, zig-zags, fine vertical and/or horizontal etched banding, or various combinations of these. Never with strong spiral sculpture and many specimens are eroded or encrusted with algae depending on the local habitat (e.g., protected shore vs. wave-exposed shore). The Interior of the shell is nearly always purple (Keep and Longstreth 1935).

General Morphology: Shelled gastropods can crawl and burrow using a muscular **foot** and have a head with **eyes** and **tentacles**, a mantle (which secretes the **shell**) and a **radula** that is composed of many teeth for tearing and rasping algae. Gastropods are characterized by torsion, where the body rotates early in development such that the visceral mass (e.g., anus, mantle cavity) is directly above the foot (rather than posterior to) (McLean 2007). The Littorinidea are small-shelled snails with a rounded peristome

(see Plate 378, Reid 2007). Two local species in the family Littorinidae, *Littorina scutulata* and *L. plena*, are morphologically very similar and differentiating them requires examination of penis morphology (see Fig. B2, supplemental images on our website, and **Possible Misidentifications** in this text).

Shell: The pattern on a typical *L. scutulata* has blue-green checks with a brown undertone and larger checks as opposed to the smaller checks of *L. plena* shells. Individuals exhibit a range of shell patterns and colors including a solid purple/black, although to a lesser degree than *L. plena* (Reid, 1996). Other reported differences include the presence of a basal ridge and a distinct light-colored basal band in the body whorl of *L. scutulata* which is absent in *L. plena* (Rugh, 1997; Hohenlohe and Boulding, 2001). Shells should be wet to fully examine colors and patterns.

Shape: Shells are conical in shape, with four whorls, lacking a columellar groove (inner lip) or chink. The shells of *L. scutulata* are large and narrow, with a tall spire and narrower aperture (Hohenlohe and Boulding 2001) (Fig. A1). Shell shape is known to vary depending on local conditions; e.g., snails on wave-exposed shores have shorter, thinner shells with a larger aperture (allows a larger foot to help prevent dislodgment) whereas snails on protected shores have larger, thicker shells with a smaller aperture (reduces predation by crabs, Rugh 1997)

Interior: *Littorina* spp. lack posterior or metapodial tentacles, having only cephalic tentacles (Carlton and Roth 1975) (see dissection, Fig. A3).

Exterior:

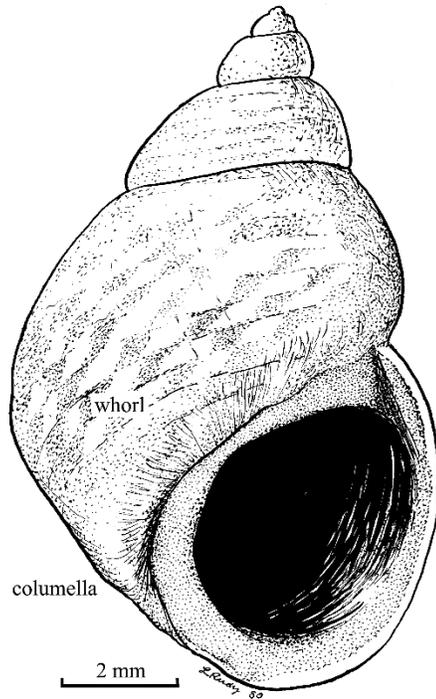
Aperture:

Inner (Columella) and Outer Lip:

Umbilicus:

Figure A

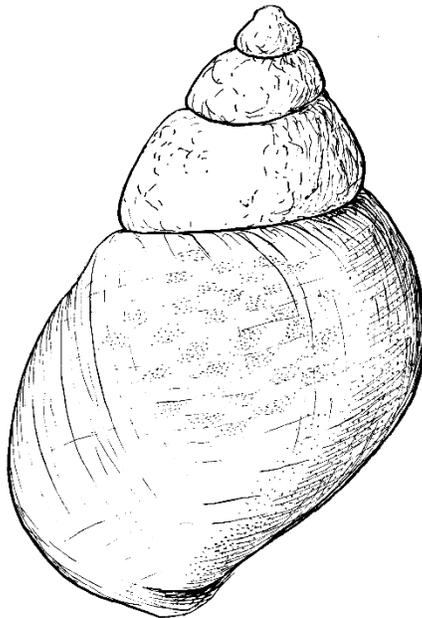
Littorina scutulata and *plena*



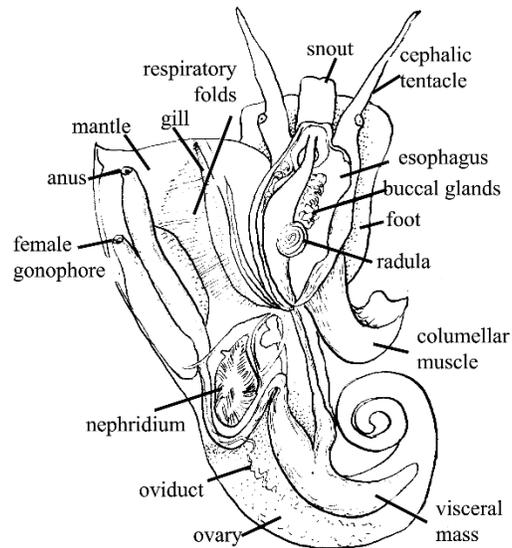
1. *Littorina scutulata* and *plena* (anterior view, H: 9mm) x12: conical, four whorls; no columellar groove; surface checkered, interior purple.



1a. Operculum.



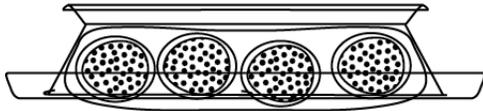
2. (Posterior view) x12.



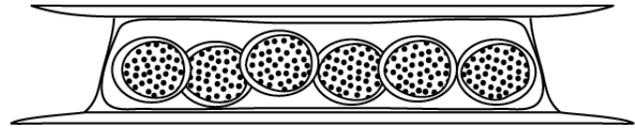
3. Dissection of female *Littorina* sp.: mantle cut, turned over (Hyman, 1967; Souleyet, 1852).

Figure B

Littorina scutulata and *plena*



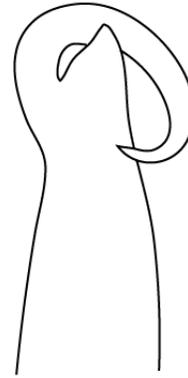
1a. *L. scutulata* egg case.



1b. *L. plena* egg case.



2a. *L. scutulata* penis.



2b. *L. plena* penis.



3a. *L. scutulata* tentacle.



3b. *L. plena* tentacle.

Illustration by Jenna Valley

Tentacles: The tentacles of *L. scutulata* have incomplete transverse bands (often alternating) with flecks (Fig. B3).

Eyes:

Siphons:

Foot:

Operculum: Solid, horny, and brown operculum with spiral lines originating in the bottom half (Fig. A1a).

Radula:

Possible Misidentifications

Snails in the genus *Littorina* (family Littorinidae) are very common members of the intertidal, however their variation in shell morphology renders species difficult to differentiate. Species level identification requires examination of the penis and pallial oviduct (Reid 1996, 2007, Fig. B2 and supplemental images on our website). A similar but smaller genus of another family is *Lacuna*, the small 'chink' shell, which has a groove, or chink, between the large whorl and the columella; *Littorina* lacks this groove. The Lacunidae are often found in eelgrass, (*Littorina* is not), and are never in the upper intertidal area, as *Littorina* often is (Kozloff 1974a).

There are seven species in the genus *Littorina* locally. Of those species, at least three have solid shell, and the absence of columellar groove found in *L. plena*. *Littorina planaxis* is an inhabitant of the outer intertidal rocks, although found in Puget Sound, and in more marine parts of Oregon's estuaries (occasionally). It is stout and globose, and usually larger than *L. scutulata* (Brusca and Brusca 1978), with a broad, flat, polished columella (Keep and Longstreth 1935). *Littorina planaxis* is essentially a southern form, although it does occur occasionally in Puget Sound (Kozloff 1974b), and its niche is generally taken over northwards at about Cape Arago, Oregon, by *Littorina sitkana* (Ricketts and Calvin 1971). *Littorina sitkana*, a fat, globose littorine, has a rounded columella, strong spiral ridges on its whorls and can be white to black, but is often a yellowish brown (Keep and Longstreth 1935). A smaller variety was formerly called *L. rudis*. It can be strongly striped, or rough and striated. It is fairly common in salt marshes, and can be up to 15 mm tall (Kozloff 1974a).

Littorina (Algamorda) newcombiana (= *subrotundata*) is a small, rare, salt marsh

littorine originally thought to be a freshwater snail. It is light-colored, with four rounded whorls, usually striped; the shell is smooth, thin and covered with a brown periostracum and the aperture is almost circular. It is only about 5 mm long, and has a simple gap, (not a groove) between the whorl and the columella (Keen and Coan 1974). It is found quite high in the intertidal area of the marsh.

Littorina littorea, is an Atlantic species introduced into California bays 100 years ago; it is quite thick-shelled, globose and colored brown to black, with fine dark spiral bands (Abbott 1968). This species has not yet been reported from Oregon (Carlton and Roth 1975).

Ecological Information

Range: Type locality is Puget Sound, Washington (Mastro et al. 1982). Known range from Sitka, Alaska to Cabo San Lucas, Baja California.

Local Distribution: Local distribution in outer coast and bays including Coos Bay, South Slough, and the Siuslaw River, near Florence (Matthews 1979).

Habitat: Snails are often found on rocks and pilings on both the rocky outer coast and protected shores, however, *L. scutulata* is reported to be most abundant on the outer coast and is rarely, if ever, found in eelgrass (Kozloff 1974a). Individuals are very tolerant of near-terrestrial conditions (Brusca and Brusca 1978).

Salinity: Found near full sea water on the open coast, as well as in conditions of somewhat reduced salinity (Carlton and Roth 1975). This species does not penetrate upper (and fresher) parts of estuary (Coos Bay). The salinity tolerance ranges from 22–24 (Brusca and Brusca 1978).

Temperature: Occurs over a wide range.

Tidal Level: Individuals are not found more than a few feet above high tide line but are found at higher levels in salt marshes (Kozloff 1974b). *Littorina* spp. are "just above the reach of the waves, along the shores of the entire bay" (San Francisco, California, Packard 1918).

Associates:

Abundance: Individuals are relatively common in rocky areas (Brusca and Brusca 1978). *Littornia plena* and *L. scutulata* are probably the most common littorine in bays,

as well, at least in more open coastal habitats.

Life-History Information

Reproduction: Dioecious (separate sexes) with internal fertilization and most copulation occurs in spring and summer, *en masse*, with a spawning season of April to early October. Sexual maturity occurs when shells are ~2–3 mm in height (by 1 yr of age) and produce negatively-buoyant pelagic egg cases, the morphology of which can be a reliable species indicator (Fig. B1 and supplemental images on our website). At 12–14°C, *L. scutulata* veligers hatch after 9 days with an initial size of ~145 µm. The planktonic period of the planktotrophic veligers can last 4+ weeks, although competency to settle can be reached by 3 weeks (Hohenlohe 2002). Fecundity reports vary but *L. scutulata* has been found to be capable of producing an average of 7,000 eggs over a two-week period (Murray, 1979; Hohenlohe, 2002). Egg cases contain pink embryos, although other colors in different regions have been reported (Buckland-Nicks and Chia, 1973) and random color variations within a region are sometimes encountered. *Littorina scutulata* capsules are smaller than *L. plena* at ~800 µm in diameter, with one rim noticeably larger than the other (the smaller rim often being upturned slightly), and have ~1–11 embryos (compared to up to 47 embryos in *L. plena*) (Fig. B, 1a and supplemental images on our website). A third egg case is also produced and exhibits a morphology with only one rim. The number of embryos per capsule may vary geographically (Hohenlohe 2002). The penis can be observed by grasping the spire of a submerged snail positioned aperture-up, providing a surface for the snail to grab onto (e.g., probe), and gently pulling away. The penis is orange-pink in color and is attached just behind the base of the right tentacle. The penis in *L. scutulata* gradually tapers with a very slight bifurcation at the tip (Fig. B2 and supplemental images on our website). The pallial oviduct in females is also distinctive but requires removal of the shell to be seen.

Larva:

Juvenile:

Longevity: The lifespan of *L. scutulata* is estimated to be at least 7 years (Behrens 1974).

Growth Rate: Under favorable conditions, *L. scutulata* can increase its bodyweight by 7% in 2 months (Behrens, 1974).

Food: Herbivorous. Littorines use their radula to rasp microscopic (e.g., *Endocladia*, unicellular green and blue green algae, diatoms), and particularly macroscopic (e.g., *Cladophora*, *Pelvetia*, *Rhodoglossum*) algae from rocks (Castenholz 1961; Dahl 1964).

Predators: Crabs, fish, birds, and predatory gastropods.

Behavior: Individuals live in a "home territory", i.e., they stay in a small area near a certain pool and "emerge by night, and submerge by day." (Abbott and Haderlie 1980). Snails are generally active when submerged and are often found clustered in groups and/or in crevices during the low tide.

Bibliography

1. ABBOTT, D. P., and E. C. HADERLIE. 1980. Prosobranchia: marine snails. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
2. ABBOTT, R. T. 1968. Seashells of North America; a guide to field identification. Golden Press, New York.
3. BRUSCA, G. J., and R. C. BRUSCA. 1978. A naturalist's seashore guide. Mad River Press, Arcata, CA.
4. BUCKLAND, J., F. S. CHIA, and S. BEHRENS. 1973. Oviposition and development of two intertidal snails, *Littorina sitkana* and *Littorina scutulata*. *Canadian Journal of Zoology*. 51:359-365.
5. CARLTON, J. T., and B. ROTH. 1975. Phylum mollusca: shelled gastropods, p. 467-514. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
6. CASTENHOLZ, R. W. 1961. The effect of grazing on marine littoral diatom populations. *Ecology*. 42:783-794.
7. DAHL, A. L. 1964. Macroscopic algal foods of *Littorina planaxis* Philippi and *Littorina scutulata* Gould. *The Veliger*. 7:139-143.

8. HOHENLOHE, P. A. 2002. Life history of *Littorina scutulata* and *L. plena*, sibling gastropod species with planktotrophic larvae. *Invertebrate Biology*. 121:25-37.
9. HOHENLOHE, P. A., and E. G. BOULDING. 2001. A molecular assay identifies morphological characters useful for distinguishing the sibling species *Littorina scutulata* and *L. plena*. *Journal of Shellfish Research*. 20:453-457.
10. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
11. KOZLOFF, E. N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
12. —. 1974b. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago and adjacent Regions. University of Washington Press, Seattle and London.
13. MASTRO, E., V. CHOW, and D. HEDGECOCK. 1982. *Littorina scutulata* and *Littorina plena*: sibling species of two prosobranch gastropod species conformed by electrophoresis. *Veliger*. 24:239-246.
14. MATTHEWS, R. 1979a. A comparative study of preferred salinities among South Slough snails, p. 8. Oregon Institute of Marine Biology.
15. —. 1979b. A comparative study of preferred salinities among South Slough snails, p. Book: 2.
16. —. 1979c. A comparative study of preferred salinities among South Slough snails, p. Book: 2. Vol. Fall.
17. MCLEAN, J. H. 2007. Gastropoda, p. 713-739. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
18. —. 2017. Gastropoda, p. 713-753. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
19. MURRAY, T. 1979. EVIDENCE FOR AN ADDITIONAL LITTORINA SPECIES AND A SUMMARY OF THE REPRODUCTIVE-BIOLOGY OF LITTORINA FROM CALIFORNIA. *Veliger*. 21:469-474.
20. PACKARD, E. L. 1918. Molluscan fauna from San Francisco Bay. *Zoology*. 14:199-452.
21. REID. 2007. *Littorina*, p. 761-766. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
22. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
23. RUGH, N. S. 1997. Differences in shell morphology between the sibling species *Littorina scutulata* and *Littorina plena* (Gastropoda: Prosobranchia). *Veliger*. 40:350-357.

Updated 2016

J. Valley and T.C. Hiebert

Littorina sitkana

The Sitka littorine

Phylum: Mollusca
Class: Gastropoda, Prosobranchia
Order: Mesogastropoda
Family: Littorinidae

Description

Size—to 15 mm (Kozloff 1974b); but usually under 12.5 mm (Ricketts and Calvin 1971); Coos Bay specimens: 4-9 mm, average about 7 mm.

Color—rough variety (fig 1) can be solid colored: plain buff or gray. A smoother variety (figs 2, 3), has strong spiral sculpture appearing as horizontal bands, especially on the largest whorl—brown to yellow or orange: these bands can be visible inside aperture and are usually fainter on upper whorls. Animal white, with black on tentacles and snout (fig 4).

Shell Shape—turbinate, thick, pointed, few-whorled (3-4); aperture rounded, outer lip acute: genus *Littorina* (Oldroyd 1924). This species stout, globose, almost as wide as high (in contrast to *L. scutulata*, for instance).

Operculum—oval (paucispiral); a solid, horny, trap door (fig 1).

Columella—rather flattened inner lip, not perforated: genus *Littorina*; rounded, upper columella is flush with 4th whorl (fig 2a): no gap between columella and whorl: genus *Littorina*.

Animal—white, with cephalic tentacles only (fig 4), no metapodial, or foot tentacles (see *Lacuna porrecta*, fig 5).

Possible Misidentifications

Littorines are turbinate, thick, pointed and few-whorled, with a rounded aperture and an acute outer lip. The columella is rather flattened but flush (appressed) with 4th whorl, and lacks a columellar groove. There are 3 other species of genus that might be confused with *L. sitkana* in Oregon estuaries:

Littorina scutulata is taller than wide, with a purple interior and often with a checkerboard pattern on its whorls (never with a strong spiral sculpture). It is found on wrack, and rarely in saltmarshes, where *L. sitkana* predominates.

Littorina planaxis is stout, like *L. sitkana*, and usually quite a bit bigger; its surface is plain, without spiral sculpture; it has a white band inside the aperture, and a characteristic

flat, roughened area between the columella and the 4th whorl. It is an outer coast, rocky shore species.

The introduced European periwinkle, *Littorina littorea*, has been found in San Francisco and Trinidad Bays. It is thick shelled, smooth, dark brown to black, with many very fine horizontal lines.

Littorina (Algamorda) newcombiana belongs to an unusual subgenus with a simple chink between the columella and the largest whorl. It is very small: to 6 mm, but averaging 3.5 mm, tall, with a smooth shiny surface covered with a brown periostracum. Its color is tan or white, with brown or black horizontal stripes at times on the largest whorl. Small specimens of *L. sitkana* can look very like *L. (A.) newcombiana*; the important differences are the simple chink next to the columella, the taller profile, small size and lighter base color of *L. (A.) newcombiana*. This latter, like *L. sitkana*, is a salt marsh inhabitant, although it is found very high in the tidal zone.

Another similar genus is *Lacuna*, the chink snail, quite tiny (2-4 mm) and distinguished from *Littorina* sp. chiefly by a definite groove or gutter between the columella and the whorl. Two species, *L. porrecta* (which see) and *L. marmorata*, have been found in our area, but usually in eelgrass, not in *Salicornia* marshes.

Ecological Information

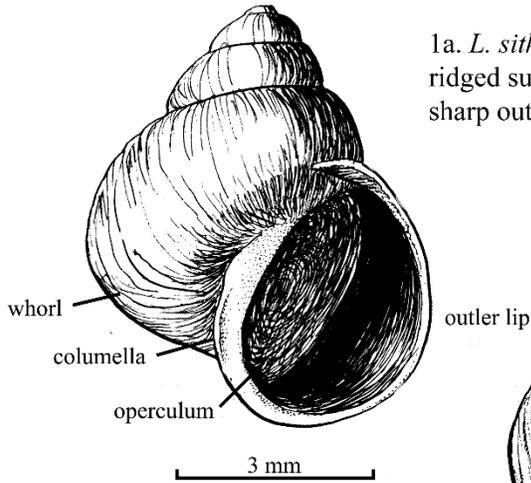
Range—southern limit seems to be about Cape Arago, near Coos Bay. North to Bering Sea (Oldroyd 1924). Not included in California keys.

Local Distribution—Coos Bay: South Slough.

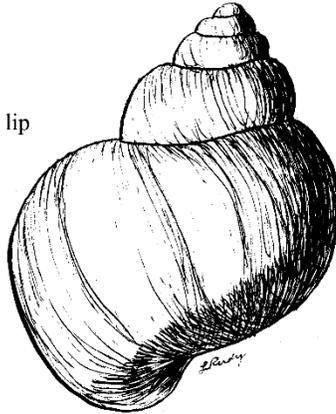
Habitat—quiet areas of *Salicornia* marshes under debris and marsh weed. Seems to need less protection than other thinner snails (Matthews 1979). In Puget Sound, found with barnacle/mussel association on or under rocks, as well as in marshes (Kozloff 1974b).

1. *Littorina sitkana* (H: 6mm, W: 5mm) x10:
solid, rough variety, almost as high as wide.

Littorina sitkana

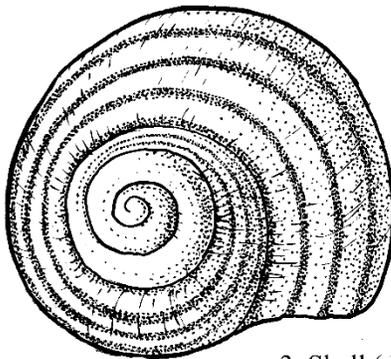


1a. *L. sitkana* (anterior view): solid color, ridged surf, rounded aperture; oval operculum; sharp outer lip; columella oppressed to fourth whorl.

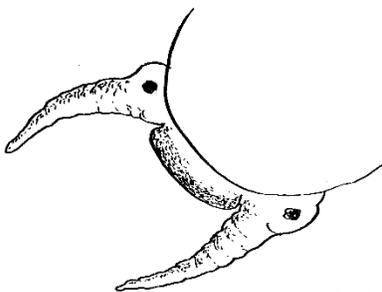
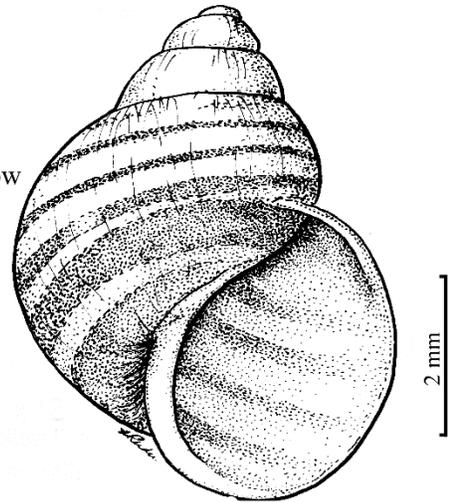


1b. *L. sitkana* (posterior view): shell thick, turbate, 3-4 whorls.

2. Smooth variety x12:
strong brown and yellow lines visible on inside.

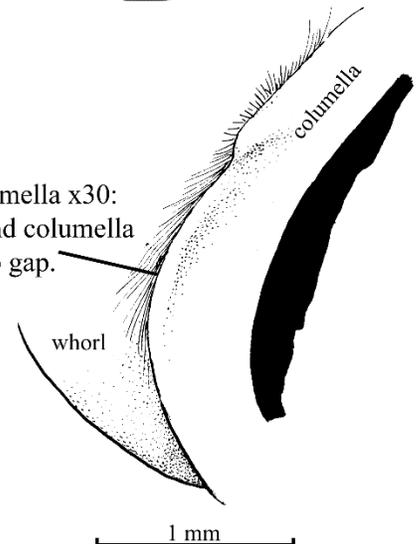


3. Shell (dorsal view).



4. Animal (dorsal view).

2a. Columella x30:
whorl and columella flush, no gap.



Salinity—Littorinidae generally can withstand salinity changes well (Keen et al 1942): conditions that can prevail in salt marshes. Prefers salinity of 24 ‰ or saltier; found at 23-30 ‰ (Matthews 1979).

Temperature—intertidal saltmarsh temperatures can vary greatly: *L. sitkana* adapts well.

Tidal Level—near the high-tide mark (Kozloff 1974b).

Associates—sphaeromid isopods, amphipod *Traskorchestia traskiana*, pulmonate snail *Ovatella myosotis*, tiny snail *Assimineia californica*, other littorines, *L. scutulata*, *L. (A.) newcombiana*. On rocks (Puget Sound): *Balanus*, *Mytilus*.

Quantitative Information

Weight—

Abundance—often the dominant small gastropod in salt marshes.

Life History Information

Reproduction—dioecious (separate sexes); small egg capsules can be seen about one month after copulation (*Littorina* sp.) (Ricketts and Calvin 1971).

Growth Rate—

Longevity—

Food—herbivorous; scrapes algae from substrate with radula.

Predators—

Behavior—

Bibliography

1. KEEN, A. M., E. COAN, and C. L. DOTY. 1942. An annotated check list of the gastropods of Cape Arago, Oregon. *Studies in Zoology*. 13.
2. KOZLOFF, E. N. 1974b. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago. University of Washington Press, Seattle & London.
3. MATTHEWS, R. 1979. A comparative study of preferred salinities among South Slough snails. Oregon Institute of Marine Biology (University of Oregon).
4. OLDROYD, I. S. 1924. Marine shells of Puget Sound and vicinity. University of Washington Press, Seattle.

5. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.

Updated 1983

Juga plicifera

Graceful keeled horn snail

Phylum: Mollusca
Class: Gastropoda
Order: Mesogastropoda
Family: Pleuroceriadae

Description

Size—"small to medium", to 35 mm long (Clarke 1981). Illustrated specimen, (Columbia River), (incomplete as drawn): 16 mm long (fig. 1).

Color—shell pale dusky grey; animal with dark transverse stripes on head and tentacles (not shown) (Clarke 1981). Periostracum blackish or brown.

Shell Shape—turriform (many-whorled, slender spired), dextrally coiled. About 15 whorls; early ones usually corroded (Clarke 1981).

Sculpture—10 to 12 axial plicae (raised ribs) on each whorl. (Plicae also described as sigmoid (C-shaped) growth rests, or as varices.) Fine collabral cords (i.e. conforming to shape of outer lip at an earlier growth stage (Clarke 1981)) (fig. 1).

Aperture—rounded below, acutely angled above (Clarke 1981); outer lip simple, entire, not notched (figs. 1, 2).

Columella—smooth (not twisted); with broad canal below it (Clarke 1981) (fig. 2).

Operculum—typical of Prosobranchia: ovate, corneous (horny), with spiral growth lines; "paucispiral," i.e. with few whorls - about 3 (Clarke 1981) (fig. 3).

Radula—(not shown); central tooth without basal denticles (Ward and Whipple 1966): family Pleuroceridae. 7 teeth/row, in pattern of 2-1-1-2, each multicuspid.

Animal—(not shown); mantle border not fringed (Ward and Whipple 1966); tentacles long, very narrow, tapering, with dark stripes; foot short, wide. Males lack penis (Clarke 1981).

Eggs—single or in small groups (Clarke 1981) (not shown).

Possible Misidentifications

The superfamily Cerithiacea includes many common marine snail genera - *Bittium*, *Cerithiopsis*, *Metaxis*, *Cerithidea*, etc. These are also turriform, with a smooth, unfolded columella. *Cerithidea californica*, the

California horn snail, is quite similar to *J. plicifera*, but is no longer found north of Tomales Bay, California (McDonald 1969). This species occurs in estuaries and bays, in mud, and under boards and debris. It has low axial ribs, not high C-shaped plicae; its operculum has multiple spirals, not just a few. It tolerates brackish water, but not fresh water.

The genus *Juga* is distinguished by its lack of the apertural notch common to many of the Cerithiacea genera. *Juga* is separated from *Goniopsis* and *Pleurocera* partly by its eggs, which are single or in small groups, not massed, and by its genitalia (the males have no penis) (Clarke 1981). *Pleurocera*, found in the eastern U.S., has a twisted columella, not a smooth one (Ward and Whipple 1966). *Goniobasis*, to which *J. plicifera* belonged until recently (Taylor 1966), is shorter than *Juga*, and has fewer whorls (Clarke 1981). *J. plicifera* is the only species of the genus in the northwestern U.S. (Clarke 1981). Also synonymized with *J. plicifera* is *J. sificula*, which was formerly believed to be a different species because it is stouter, with stronger ribs and a wider apical angle (Henderson 1929).

J. acutifilosa Stearns, the sharp lined river shell of northern California lakes, has strong spiral keels (Keep 1935), and is probably extinct (Clarke 1976).

Ecological Information

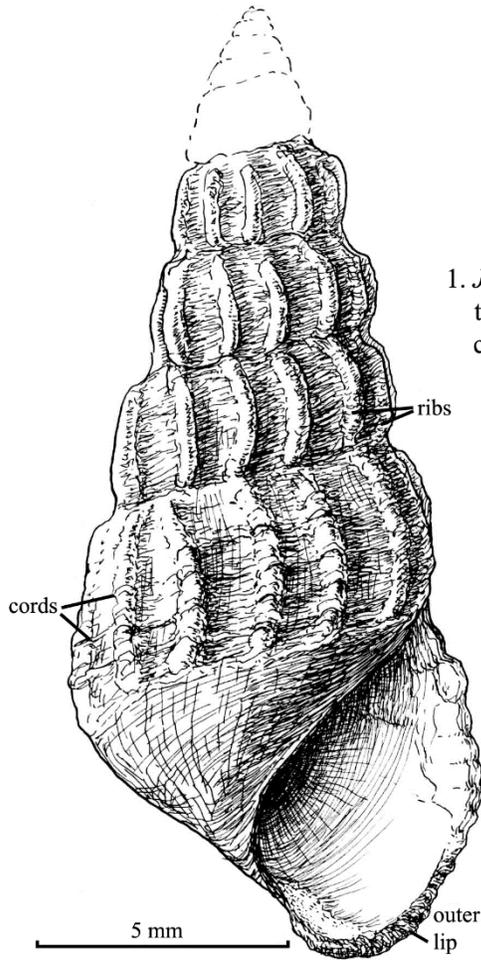
Range—Olympic Peninsula, Washington; Columbia River and other drainages south to California. Possibly Vancouver Island.

Local Distribution—Columbia River, lower reaches; also Tahkenich Lake, near Florence, Oregon (Douglas Co.).

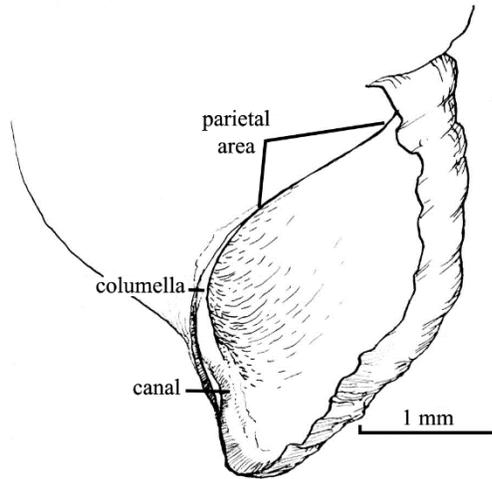
Habitat—muddy-sand bottoms of small and medium lakes; also slow flowing streams (Clarke 1981). Likes cool clear water, green algae (Keep 1935).

Salinity—considered a freshwater species, it is also found in the lower Columbia River.

Juga plicifera



1. *Juga plicifera* x8:
turriform; axial ribs, spiral
cords, dusky grey.



2. Aperture x12:
rounded below, acutely angled above;
parietal area attenuate, imperforate;
columella smooth, canal below it.



3. Operculum x12:
ovate corneous; a few spiral
growth lines.

Temperature—
Tidal Level—
Associates—

Quantitative Information

Weight—
Abundance—

Life History Information

Reproduction—family is oviparous (Henderson 1929); no external verge (male organ).

Growth Rate—

Longevity—

Food—most of family are bottom feeders; some feed on plants, algae, dead vegetation (Clench and Turner 1956).

Predators—

Behavior—

Bibliography

1. CLARKE, A. H. 1981. The freshwater molluscs of Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Canada.
2. CLENCH, W. J., and R. D. TURNER. 1956. Review of freshwater mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwannee River. Bulletin of the Florida Museum. 3:97-240.
3. HENDERSON, J. 1929. Non-marine Mollusca of Oregon and Washington. [University of Colorado], Boulder, Colo.
4. KEEP, J. B. J. L., and ED. 1935. West coast shells; a description in familiar terms of principal marine, fresh-water, and land mollusks of the United States, British Columbia, and Alaska, found west of the Sierra. Calif., Stanford University Press; London, H. Milford, Oxford University Press, Stanford University.
5. MACDONALD, K. B. 1969. Molluscan faunas of Pacific coast salt marshes and tidal creeks. The Veliger. 11:399-405.
6. TAYLOR, D. W. 1966. Summary of North American Blancon nonmarine

mollusks. Malacologia. 4:1-172.

7. WARD, H. B., and G. C. WHIPPLE. 1963. Fresh-water biology. John Wiley & Sons; New York.

Updated 1988

Callianax biplicata

The purple olive

Phylum: Mollusca
Class: Gastropoda
Order: Neogastropoda (=Stenoglossa)
Family: Olividae

Description

Size—large for family: to 30 mm long (Carlton and Roth 1975); mature at 16 mm (Edwards 1968); males larger than females. Width usually about twice as high as wide (Kozloff 1974a). This specimen 18 mm high, 9 mm wide.

Color—gray, purple fasciole (band) at base offset with dark line (fig. 1); faint vertical striations, but surface otherwise polished, unsculptured: genus *Olivella* (*Callianax*) (Carlton and Roth 1975).

Shell Shape—stout, robust, sub-cylindrical; spire only slightly elevated; 5-6 whorls. Body whorl convex, nearly flat near thin straight outer lip; aperture elongate, triangular, with anterior notch (fig. 2).

Columella—strong callus, with a fold of 2 incised spiral lines or plications in lower portion: sp *biplicata* (fig. 2).

Operculum—small, horny, thin, half ovate, apical nucleus (not figured).

Animal—eyeless; foot plow-shaped, for burrowing (McLean 1969). Long siphon for water intake (fig. 3). Radula with 3 teeth to the row: Neogastropoda (not figured).

Eggs and Young—egg like a dome-shaped hat, about 0.5 mm diameter (fig. 4a). Veliger 0.2-0.3 mm (fig. 4b) (Edwards 1968).

Possible Misidentifications

Callianax species are the only genus of the family Olividae in our north temperate waters; the larger *Oliva* is a warm water genus. The genus *Callianax* may be distinguished by its smooth surface, slight spire, elongate, notched aperture, clean sand habitat, and in *C. biplicata* by its columellar folds. At least 3 *Callianax* are found on the west coast:

Callianax baetica, slenderer than *C. biplicata* (2 ½ x as high as wide), shell tan or cream with red, brown or purple markings and lines: it can be found on protected beaches and subtidally. It is smaller than *C. biplicata*—only up to 19 mm. It is found in Puget Sound as well as in California (Kozloff 1974a; Carlton and Roth 1975).

Callianax pycna, another small olive (to 19 mm), is stout, and has brownish zig-zag lines on its whorls (Carlton and Roth 1975). It is not found in Puget Sound, but is a more southern species.

Characteristics of the family Olividae include a polished shell (indicating that the mantle often covers it), a subcylindrical, spired shell with an aperture greater than ½ the shell length. They are usually sand dwellers.

Ecological Information

Range—Vancouver Island to Magdalena Bay, Baja California: Oregonian and Californian shallow water marine faunal provinces.

Local Distribution—outer, marine portions of most bays and estuaries, including Coos Bay, Netarts (Stout 1976).

Habitat—sandy beaches and spits of bays, as well as outer coast. Can concentrate metals in tissues, apparently without harm (Morris et al 1980).

Salinity—full sea water.

Temperature—

Tidal Level—low intertidal to subtidal waters: lives in quite a wide band (Kozloff 1974b); found higher than and associated with the razor clam: *Siliqua patula*.

Associates—*Siliqua patula*; parasitic nematodes (Edwards 1969): in southern California, hydroids on spire.

Quantitative Information

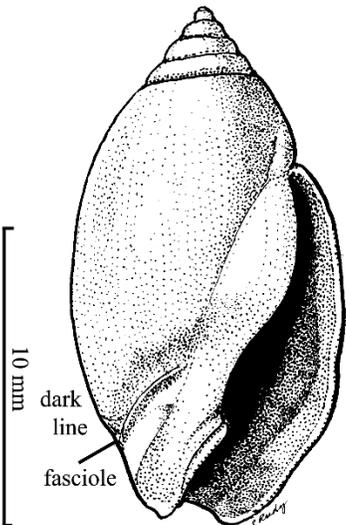
Weight—

Abundance—common intertidally (Carlton and Roth 1975).

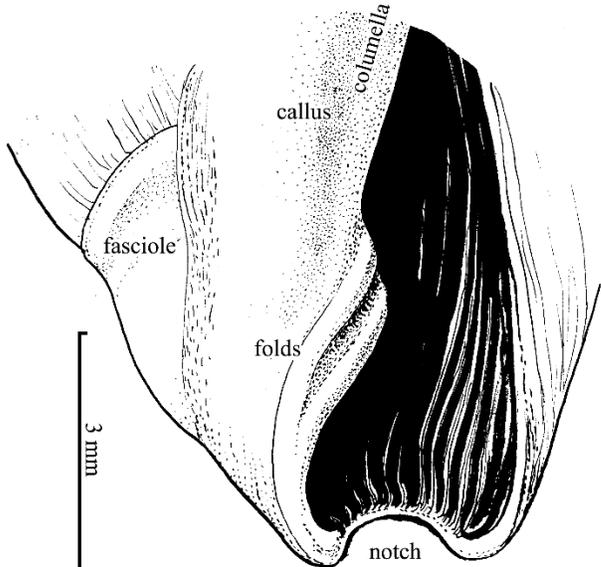
Life History Information

Reproduction—dioecious (two sexes); mating behavior observed at every low tide, all year: no 'year classes' in Oregon waters. Mate selection by chemosensory means; internal fertilization. Only sexual dimorphism observable is larger size of males. Sterility rate may be as high as 50% due to trematode infestation. Single egg cases deposited usually on empty shells; egg development

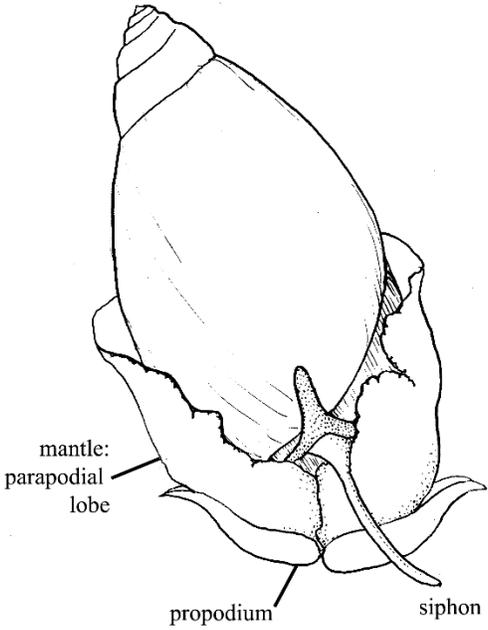
Callianax biplicata



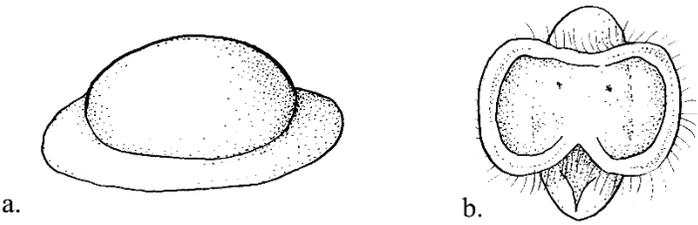
1. *Callianax biplicata* (anterior view, H:18mm) x4.5: about twice as high as wide; polished surface: gray with purple fasciole; stout, subcylindrical; slight spire; 5-6 whorls; long aperture.



2. Columella and aperture x12: columella with strong callus, two fold; aperture notched.



3. *C. biplicata* (dorsal view).



4. Egg and larva x100:
a. egg case
b. veliger (frontal view)
(Edwards, 1968).

time variable: 10-28 days (Edwards 1968).

Veligers nonpelagic: swim near substrate (Edwards 1968).

Growth Rate—to maturity (16 mm) in one year. Males grow faster than females and are larger. Growth rate varies from 0.1 mm to 9.7 mm/year (Stohler 1969). Few young reach maturity; mostly populations of older animals, which have a low mortality rate (Edwards 1969).

Longevity—possibly several years: as many as ten (Edwards 1968).

Food—family is carnivorous; scavengers animal matter; large *Callianax* will eat polychaetes (Edwards 1969).

Predators—*Pisaster brevispinus* (Coos Bay, North Spit) (Edwards 1969): small *Cancer antennarius* and *C. magister*, shorebirds, particularly gulls; fish; man, for ornament (Stohler 1969). In southern California: mollusks *Octopus*, *Polinices*, *Conus*, echinoderm *Astropecten* (Stout 1976).

Behavior— reacts to predator *Pisaster brevispinus* by crawling or by rapid upside down swimming (Edwards 1969). Trails near surface. shell partly exposed. Larger animals active at night and hide from predators during the day.

Bibliography

1. CARLTON, J. T., and B. ROTH. 1975. Phylum Mollusca: Shelled Gastropods, p. 467-514. *In*: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
2. EDWARDS, D. C. 1968. Reproduction in *Olivella biplicata*. *The Veliger*. 10:297-304.
3. ———. 1969. Predators on *Olivella biplicata*, including a species-specific predator avoidance response. *The Veliger*. 11:326-333.
4. KOZLOFF, E. N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle & London.
5. ———. 1974b. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago. University of Washington Press, Seattle & London.
6. MCLEAN, J. H. 1969. Marine shells of

southern California. [Los Angeles] Los Angeles County Museum of Natural History.

7. MORRIS, R. H., D. P. ABBOTT, and E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California.
8. STOHLER, R. 1969. Growth study in *Olivella biplicata*. *The Veliger*. 11:259-267.
9. STOUT, H. 1976. The natural resources and human utilization of Netarts Bay, Oregon. Oregon State University, Corvallis, OR.

Updated 1988

Nucella lamellosa

The wrinkled or frilled dogwinkle

Phylum: Mollusca
Class: Gastropoda, Prosobranchia
Order: Neogastropoda
Family: Thaisidae

Description

Size—to 50 mm (California)(Morris et al. 1980), 100 mm Puget Sound and north (Kozloff 1974a); largest specimen figured, 54 mm (fig. 1). Largest of the *Nucella*.

Color—white to brown, some are pink, lavender or orange tan; not highly polished. Inside whitish, sometimes with color showing through.

Shell Shape—shell heavy, solid, strong; spirally coiled, fusiform (spindle-shaped). 5-7 whorls; nuclear whorl small, in-conspicuous. Spire usually high; siphonal canal relatively long for genus; aperture ovate, almost 1/2 shell length.

Sculpture—extremely variable. Spire and base have similar sculpture: genus *Nucella* (Smith and Carlton 1975, Keen and Coan 1974). Axial ribs present (fig. 1). Three chief variations with many gradations): lamellar variety with strong axial ribs, developed in quiet water specimens into frilly ruffles (fig. 4); (2) *Nucella* from rough conditions are smooth, with only faint axial sculpture (figs. 1, 3); and (3) strongly sculptured spirally with one to two strong horizontal ribs at top of each whorl and smaller ribs below; axial sculpture only between ribs. This variety has flattened and angled whorls (fig. 2) (Kozloff 1974a).

Outer Lip—thickened, smooth, without denticles on posterior portion of aperture (near anal notch)⁶; no single strong tooth on edge near anterior canal (see Possible Misidentifications). Outer lips rounding smoothly to anterior end of shell. At least one row of denticles within lip (fig. 1).

Columella—(central pillar): without folds (Kozloff 1974a); incrustated, smooth.

Suture—(between whorls): Impressed, distinct, but not a deep groove.

Anterior (Siphonal) Canal—short, but longer than other *Nucella* species; narrow, slot-like, not spout-like (i.e. with edges touching, making a closed tube: see **Possible Misidentifications**). Not separated from large whorl by revolving groove (fig. 1).

Aperture—almost 1/2 length shell; ovate to quadrate in outline, with a siphonal notch, but

no anal notch (fig. 1). Widest part of aperture (generally near its middle) at least half as wide as shell (Kozloff 1974a).

Umbilicus—small, often closed (fig. 1).

Operculum—usually large enough to close aperture; conspicuous, with strong spiral lines; with nucleus on one side (fig. 1a).

Eggs—vase-shaped, yellow, about 10 mm long; in clusters on underside of rocks (Morris et al. 1980); called "sea oats"; (fig. 1b).

Possible Misidentifications

Nucella can be distinguished from other predatory estuarine snails by its sculpture, which is the same on the whorls and spire, by the large last whorl and by the ovate aperture (about 1/2 the shell length). Unlike *Nassarius*, it has no distinct revolving furrow setting off the body whorl from the anterior canal (Keen and Coan 1974). It has no single strong tooth on the anterior margin of the outer lip, as in *Acanthina*. There are no columellar folds as in *Olivella*, *Buccinus*, etc. The siphonal canal is not spout-like, as in *Ocenebra*, and *Ceratostoma*.

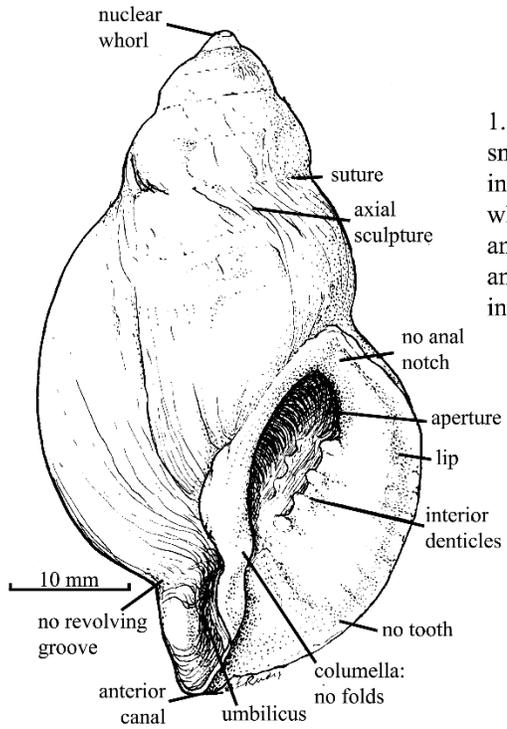
There are several species of *Nucella* in the northwest:

Nucella lima, the file dogwhelk, is a subtidal snail with about 16 alternating large and small file-like spiral ridges on the large whorl. It is fairly rare, is whitish to brown in color, short-spined and somewhat smaller than *N. lamellosa* (to 43 mm).

Nucella canaliculata, the channeled dogwhelk, is white to or orange, sometimes banded. It has a high spire, a prominent shoulder below the deep suture, and rounded spiral ridges of equal size with axial lamellae between them. It is small, to just over 30 mm. Usually found in mussel beds, it is rare in bays (Kozloff 1974a).

Nucella emarginata (which see) is the other *Nucella* most often to be found in estuaries; it usually occurs in heavier surf than *N. lamellosa*. Called the rock-dwelling dogwinkle, it is generally only up to 20 mm long. This snail has alternately large and small, often

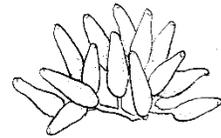
Nucella lamellosa



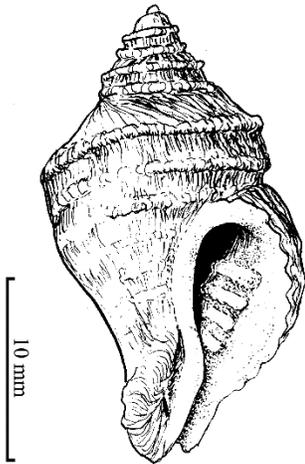
1. *Nucella lamellosa* (posterior view, H:54mm) x2: smooth variety; fusiform; 5 whorls (nuclear whorl inconspicuous); axial sculpture on both spire and body whorl; ovate aperture almost 1/2 shell length; narrow anterior canal; smooth outer lip without posterior denticles, anal notch or marginal tooth; columella without folds; interior rows of denticles, umbilicus closed; suture not deep.



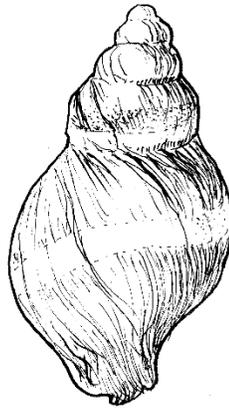
1a. Operculum x2.



1b. Egg cluster x1.



2. Spiral ribbed variation x2: 1-2 strong horizontal ribs at top of each whorl, smaller ribs below; fine axial sculpture between ribs; whorls angled, flattened.



3. Smooth, banded variation x2.



4. Frilly, lamellar variation x1: axial sculpture strong.

nodulose, spiral ridges over most of the shell. (These ridges are often obscure). It has no noticeable axial sculpture. Found in the mid- and high intertidal in mussel beds, it is easily confused with variation of *N. lamellosa* (fig. 2).

Nucella was previously called *Thais*. This name is now re-served for subtropical and tropical species.

Ecological Information

Range—Bering Strait to central California (Morris et al 1980).

Local Distribution—Coos Bay: Pigeon Point, Empire; Umpqua estuary: Ziolkouski Beach (1/2 mile from mouth).

Habitat—on rocks with mud, sand substrate; often in protected bays (Carlton and Roth 1975); below mussel beds on outer shores.

Salinity—collected at 30 ‰ salt: lower, more marine parts of bays with more constant saline concentrations.

Temperature—cold to temperate waters: geographic distribution would indicate a preference for cool temperatures. Lower part of bay does not generally have high temperatures. Smallest individuals have highest thermal limits; snails active at 0-30 °C (Bertness 1977).

Tidal Level—found at low intertidal, below other species of the genus. Largest animals lowest in tidal range (Bertness 1977).

Associates—its primary prey: barnacle *Balanus*; the under-rock community: porcelain crab *Petrolisthes*, brachyuran crabs *Hemigrapsus* and *Cancer oregonensis*, chiton *Mopalia*, isopod *Idotea*, anemones *Anthopleura elegantissima* and *A. artemesia*, nudibranch *Onchidoris*, gastropod *Tegula*; *Pisaster ochraceus*. Discarded *N. lamellosa* shells are often inhabited by the hermit crab *Pagurus hirsutiusculus*.

Quantitative Information

Weight—largest collected (including shell) 28 gr. (wet).

Abundance—one of the most abundant intertidal snails of the northwest; becomes less abundant in California. By far the most common *Nucella* species in the Coos Bay estuary.

Life History Information

Reproduction—breeding in winter and spring (California) by aggregations of snails; individuals become sexually mature in 4th year, when they often return to their hatching site and join a breeding group (Morris et al. 1980); individuals tend to breed with same group. Egg capsules deposited synchronously by females; development varies with temperature: snails emerge after 140 days (at 6.8°C), after 67-91 days (9.6-11 °C). Capsules rarely contain "nurse eggs" (sterile eggs to be consumed by the developing snail larvae): nearly all eggs are fertile (Lyons and Spight 1973). Just over half of eggs reach hatching stage; high mortality among young snails: of 1000 eggs (from one female, one year), probably fewer than 10 grow to 1 year of age.

Growth Rate—varies greatly with food supply. Shell growth, type, dependent on food: barnacle diet produced heavy, stout shells.

Longevity—sexually mature at four years (Morris et al. 1980).

Food—primarily barnacles: *Balanus glandula* and *B. cariosus*, on which it is the primary predator (Puget Sound) (Kozloff 1974a). Mussels (outer shores), periwinkles and other mollusks. Radula penetrates shell of prey with aid of secretions from boring organ on foot (Morris et al. 1980).

Predators—egg capsules and young snails heavily preyed upon by other *Nucella*.

Bibliography

1. BERTNESS, M. D. 1977. Behavioral and ecological aspects of shore-level gradients in *Thais lamellosa* and *Thais emarginata*. Ecology. 58:86-97.
2. CARLTON, J. T., and B. ROTH. 1975. Phylum Mollusca: Shelled Gastropods, p. 467-514. In: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
3. KOZLOFF, E.N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle & London.

4. LYONS, A., and T. M. SPIGHT. 1973. Diversity of feeding mechanisms among embryos of Pacific Northwest Thais. *The Veliger*. 16:189-194.
5. MORRIS, R. H., D. P. ABBOTT, and E. C. HADERLIE. 1980. *Intertidal invertebrates of California*. Stanford University Press, Stanford, CA.

Updated 1983

Nucella ostrina

The rock-dwelling emarginated dogwinkle

Phylum: Mollusca
Class: Gastropoda, Prosobranchia
Order: Neogastropoda
Family: Thaisidae

Description

Size—rarely over 30 mm (Kozloff 1974a), usually up to 20 mm (Puget Sound); up to 40 mm, but rarely over 30 mm (California) (Morris et al. 1980); this specimen (Coos Bay) 20 mm. Females slightly larger than males (average 18.9 and 17.8) (Houston 1971).

Color—exterior brown and dingy white, dirty gray, yellow or almost black (if diet of mussels); yellow, black or gray periostracum in grooves between ridges; ridges sometimes white (black in this specimen). Interior: aperture and columella chestnut brown or purple.

Shell Shape—fusiform; short spire, expanded whorl. Shell thin, not heavy. 3-4 whorls; nuclear whorl inconspicuous.

Sculpture—base and spire with similar sculpture: genus *Nucella* (Carlton and Roth 1975); alternating large and small spiral ridges over most of shell, can be nodulose; sometimes ridges are obscure and surface is fairly smooth. Axial sculpture wrinkled, not prominent.

Outer Lip—thin, crenulate, not thick and layered: species *ostrina* (Oldroyd 1924). No denticles or anal notch on posterior (upper) end, no single strong tooth near anterior canal. No row(s) or denticles within lip.

Columella—excavated (ibid), arched and flattened below: species *ostrina*; no folds, (fig. 1).

Sutures—not deep (fig. 1).

Anterior (Siphonal) Canal—short: less than V aperture length: species *ostrina* (Kozloff 1974a) (fig. 1); canal narrow, slot-like, not spout-like; not separated from large whorl by revolving groove.

Aperture—wide; length more than 1/2 shell length (Oldroyd 1924). Ovate in outline, with a short anterior canal but no posterior notch (fig. 1).

Umbilicus—closed: species *ostrina* (Carlton and Roth 1975).

Operculum—dark brown with nucleus on one side (fig. 2).

Eggs—pale yellow, vase-shaped, about 6 mm high, in clusters of up to 300 capsules

(Morris et al. 1980) (fig. 4). Each capsule with 500-600 eggs. Each capsule with a longitudinal suture and a hard clear escape aperture.

Veliger—4 stages: advanced shell measures 775 μ long (LeBoeuf 1971) (fig. 5).

Possible Misidentifications

Snails of the genus *Nucella* can be distinguished from other carnivorous estuarine gastropods by their sculpture (the same on both spire and whorls), by the large body whorl and by the large ovate aperture. Other genera with a siphonal notch, and generally fusiform shape include

Olivella and *Buccinum*, which have columellar folds;

Ocenebra and *Ceratostoma* which have a spout-like siphonal canal, not a narrow-slot-like one as in *Nucella*;

Nassarius and *Searlsia* which have a distinct revolving fur-row or fossa setting off the anterior canal from the body whorl; (*Searlsia* has spiral sculpture only on the body whorl; the spire has both spiral and axial ribs);

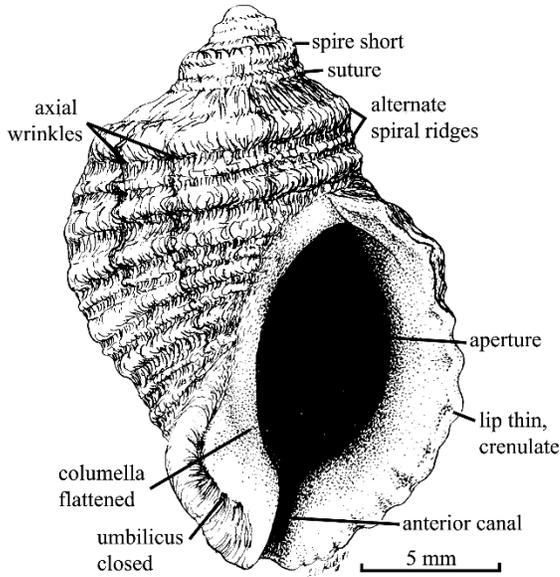
Acanthina (also from the family Thaisidae), which has a strong tooth on the anterior end of the outer lip.

There are three other species of *Nucella* in our area. Two are not likely to be found in estuarine conditions, but they do look quite a bit like *No. ostrina*:

Nucella lima, the file dogwinkle, is subtidal, short-spined, and fairly rare. It is whitish to brown, with about 15 alternating large and small file-like spiral ridges on the large whorl. It can be up to 43 mm, somewhat larger than *N. ostrina*.

Nucella canaliculata, the channeled dogwhelk, has a high spire and a prominent shoulder below the deep suture. It is light (white to orange), and sometimes banded. Its 14-16 spiral ridges are very evenly shaped and spaced. It is an inhabitant of outer shore mussel beds. Larger than *N. ostrina*, it averages 26.5 mm (male) and 24.8 mm (female) (California) (Houston 1971).

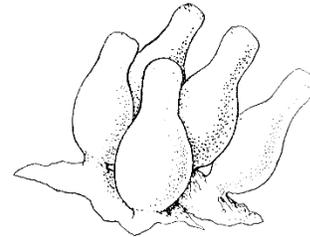
Nucella ostrina



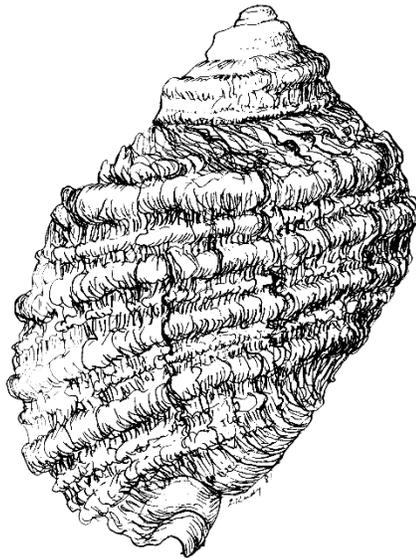
1. *Nucella ostrina* (ventral view, H: 21mm) x4:
Shell ovate, body whorl expanded, spire short;
aperture ovate, wide; sculpture: alternating large and small
nodulose spiral ridges, wrinkled axial folds; columella
flattened, unfolded; umbilicus closed; outer lip crenulate,
thin, no denticles, short anterior canal.



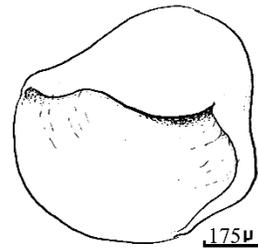
2. Operculum.



4. Egg capsules x4.



3. *Nucella ostrina* (dorsal view) x4.



5a. Advanced veliger
shell (Le Boeuf 1971).



5b. Advanced veliger
larva - fourth stage
(Le Boeuf 1971).

The third species of *Nucella* is quite likely to be found in bays: *N. lamellosa* (which see) is the most common dogwinkle in the northwest, and one of its many variations is very like *N. ostrina*. *N. lamellosa* can have strong axial ruffles, be quite smooth, or have strong horizontal ribs. In this last case, it must be carefully separated from *N. ostrina*. *N. lamellosa* has a higher spire (usually 5-7 whorls, including the tiny nuclear whorl); it is heavy, with a thick layered lip, not a thin crenulated one. There is usually at least one row of denticles inside the lip in *N. lamellosa*; its anterior canal is longer than that of *N. ostrina* (more than 1/4 aperture length). While *N. lamellosa* can have strong spiral ridges, the body whorl in this species is then often flattened and angled, not expanded as in *N. ostrina*, and the horizontal ridges themselves are not alternating large and small (compare fig. 2, *N. lamellosa*). *Nucella lamellosa* inhabits much quieter waters, as a rule, and a lower tidal range than does *N. ostrina*. Its color is usually lighter; it is rarely blackish.

Ecological Information

Range—Bering Sea south to northern Baja California, but rare below Pt. Conception (Morris et al. 1980).

Local Distribution—Coos Bay: marine portions, i.e. near bay mouth up to Fossil Point.

Habitat—almost entirely on rocky shores; in fairly heavy surf (Ricketts and Calvin 1971); also in semi-protected areas (Houston 1971). Outer shores in mussel beds, on jetties.

Salinity—full seawater; collected at 30 ‰.

Temperature—cold to temperate waters: small animals high in tidal range show great thermal resistance active at range of 0-30°C (Bertness and Schneider 1976).

Tidal Level—

Associates—its primary prey, barnacles, especially *Balanus*; mussel *Mytilus*; *Pisaster ochraceus*. Commensal flatworm *Nexilis epichitonius* found in specimens on Coos Bay entrance jetty (Holliman and Hand 1962).

Quantitative Information

Weight—1.5 gm (wet).

Abundance—common to abundant (Carlton and Roth 1975); much less common in inner bay than *N. lamellosa* (Coos Bay).

Life History Information

Reproduction—spawn throughout the year (Bodega Bay, Calif.), but most activity is in November-February. Little hermaphroditism (Houston 1971). Spawning not salinity, photoperiod- or temperature-related (Houston 1971). Females gregarious (groups to 20), deposit egg capsules in clusters. Each female lays 8-9 capsules; stalked capsules have about 200-300 eggs each (ibid), many of which may be sterile nurse eggs which are consumed by developing larvae. Veligers swim in capsule fluid and metamorphose into snails about 1.1 mm long, emerging from plug at top of capsule (ibid). Pacific northwest hatchlings number about 10-20 per capsule average; Bodega Bay about 5% hatch (10-15) (ibid): 11.

Growth Rate—Pacific northwest: 2.5-3 months from egg deposition to hatching; possibly more rapid development farther south (Morris et al. 1980).

Longevity—

Food—prefers mussels *Mytilus edulis* and *M. californianus*; also barnacles *Balanus*, *Pollicipes*, *Chthamalus*; limpets *Collisella*, as well as herbivorous gastropods *Tegula funebris* and *Littorina*. Feeding is by drilling with the radula, inserting the proboscis, and feeding on the soft body within. Species *N. ostrina* shows a wide food preference, but individuals seem to be consistent in diet (Morris and Abbott et al 1980).

Predators—adult snails prey on eggs.

Behavior—presence of *N. ostrina* elicits several escape responses from prey *Mytilus edulis*: gaping, spontaneous valve closure, foot activity, byssal fixing (Wayne 1980).

Bibliography

1. BERTNESS, M. D., and D. E. SCHNEIDER. 1976. Temperature relations of Puget Sound thais in reference to their intertidal distribution. *The Veliger*. 19:47-78.
2. CARLTON, J. T., and B. ROTH. 1975. Phylum Mollusca: Shelled Gastropods, p. 467-514. *In*: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.

3. HOLLIMAN, J. T., and C. HAND. 1962. A new species, genus, and family of marine flatworms (Turbellaria: Tricladia, Maricola) commensal with mollusks. *The Veliger*. 5:20-22.
4. HOUSTON, R. S. 1971. Reproductive biology of *Thais emarginata* (Deshayes 1839) and *Thais canaliculata* (Duclos 1832). *The Veliger*. 13:348-357
5. KOZLOFF, E.N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle & London.
6. LEBOEUF, R. 1971. *Thais emarginata* (Deshayes): Description of the veliger and egg capsule. *The Veliger*. 14:205-211.
7. MORRIS, R. H., D. P. ABBOTT, and E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California.
8. OLDROYD, I. S. 1924. Marine shells of Puget Sound and vicinity. University of Washington Press, Seattle.
9. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
10. WAYNE, T. 1980. Antipredator behavior of the mussel *Mytilus edulis* (Abstract). *American Zoology*. 20:789.

Updated 1983

Hermisenda crassicornis

An opalescent aeolid nudibranch

Phylum: Mollusca
Class: Gastropoda
Order: Nudibranchia
Family: Facelinidae

Description

Size—30 mm to 80 mm long (Beeman and Williams 1980); this specimen (Coos Bay) 50 mm.

Color—ground color often white, transparent, but can be yellow or green (MacFarland 1966), with opalescent white or blue line around foot, down each oral tentacle, and down back, where it is double and encloses 2 orange spots (McDonald 1975). Line can form diamond shape between first cerata. Cerata cores (digestive glands) brown or reddish; cerata tips orange, except for clear very tip: typical (Beeman and Williams 1980). These specimens with vertical white stripe on cerata. Many cerata color variations: rust, red, black, brown, green (Keen 1971).

Body—“aeolid”; an oblong, flat-bottomed form, with rhinophores, cerata, tail, but without posterior plume of branched gills (fig. 1).

Rhinophores—long; with 8 - 24 slanted, faint “leaves” or rings (Farmer 1980); “weakly perfoliate” (McDonald and Nybakken 1980) or annulate, otherwise solid (fig. 1). Color: as ground.

Foot—split in front (“anteriorly bilabiate”) (Farmer 1980); lateral angles produced into horns (fig. 1); foot extends posteriorly into long, pointed tail. Foot corners or horns also called “pedal tentacles” (Kozloff 1974a).

Cerata—large, conical, in 11 clusters of transverse rows (Farmer 1980) covering animal's back. Cerata begin posterior to rhinophores (Beeman and Williams 1980), are longest in median region of 1st 2 groups (Behrens 1980). Each cerata with a core of digestive gland (fig. 1), and at tip a cnidosac, which collects nematocysts from cnidarian prey (MacFarland 1966).

Oral Tentacles—usually present, order Nudibranchia (McDonald 1975). Long, white, pointed (fig. 1).

Gills—none (fig. 1). Cerata serve as gills.

Eyes—small, black; posterior to bases of rhinophores (fig. 1). With only 5 large cells: used in neurological studies (Beeman and Williams 1980).

Radula and Jaws—ribbon of horseshoe-shaped teeth; each central cusp with a single row of up to 28 teeth; 4-6 sharp spines on either side of middle cusp, whose under surface has up to 15 small points (MacFarland 1966) (fig. 4).

Mouth—jaw border with up to 50 denticles (MacFarland 1966). (Mandibles not figured.)

Genital Openings—genital apertures on low posterior part of 1st group of cerata (MacFarland 1966) (not visible as drawn, but see arrow, fig. 1).

Anus—tubular, on right, between 2nd and 3rd groups of cerata (fig. 1) (MacFarland 1966). Concealed anus: tribe Cleioprocta (MacFarland 1966). Anus more anterior than in Aeolididae (Keen 1971).

Renal Pore—lateral, between 1st and 2nd group of cerata (not visible, but see arrow, fig. 1).

Eggs—in pink sausage-like string; each 1 mm diameters, attached through much of its length to substrate. String makes tight counterclockwise spiral. Each capsule can have 1 – 4 eggs (Beeman and Williams 1980) (fig. 5).

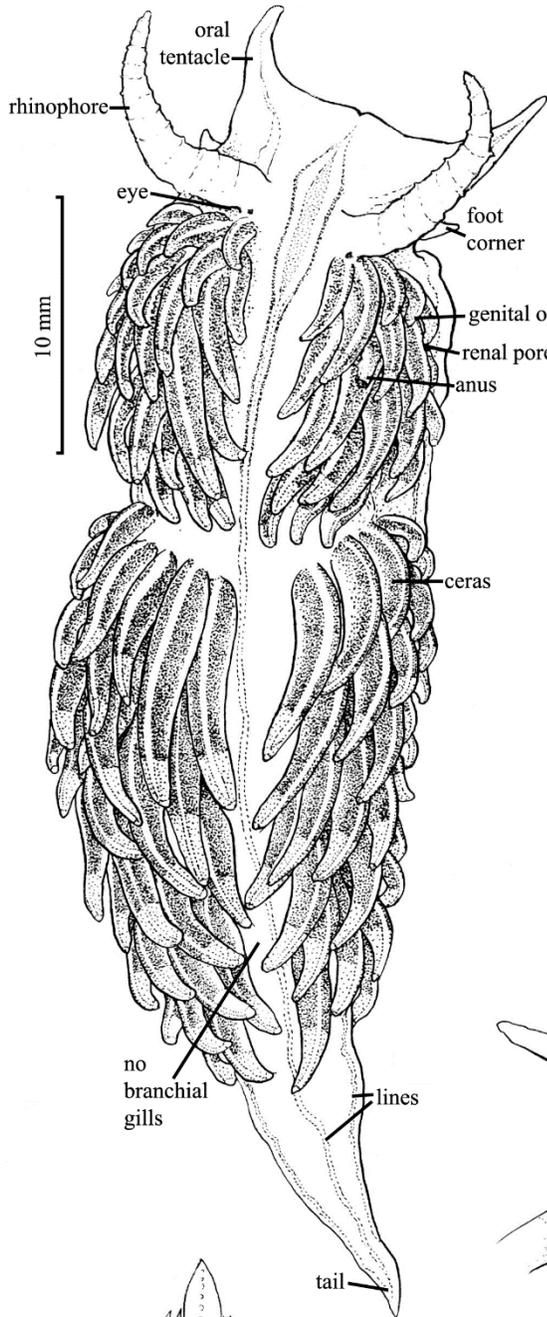
Possible Misidentifications

Nudibranchs can be separated from other apparently shell-less opisthobranchs by their radulae and jaws (they are carnivorous), and by their rhinophores, which are not rolled as they are in sacoglossans. Nudibranchs also have oral tentacles. In addition, they have lost all shell and opercula (as adults) as well as mantle cavity and gills. (Some may have secondary gills on their backs (McDonald and Nybakken 1980)). Nudibranch genital openings are on the right side.

The nudibranchs in *Hermisenda's* suborder, Aeolidiacea, are relatively small, long, and narrow, gill-less, and have cerata. They feed partly on cnidaria, and are able to store nematocysts in their cerata (Keen 1971).

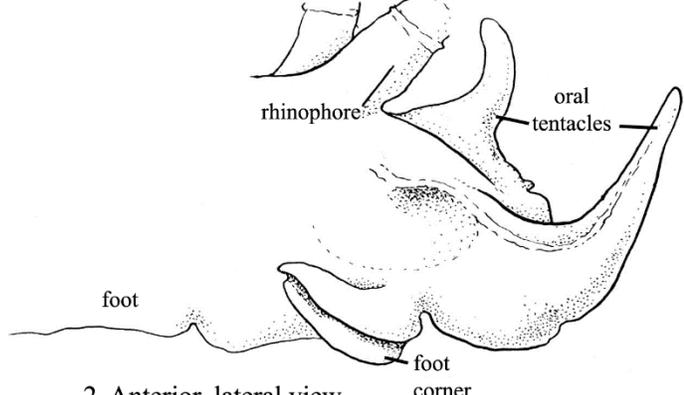
The nudibranchs in the other major suborder, Doridacea, are larger, with a large flat foot, thick mantle and obvious gills

Hermisenda crassicornis



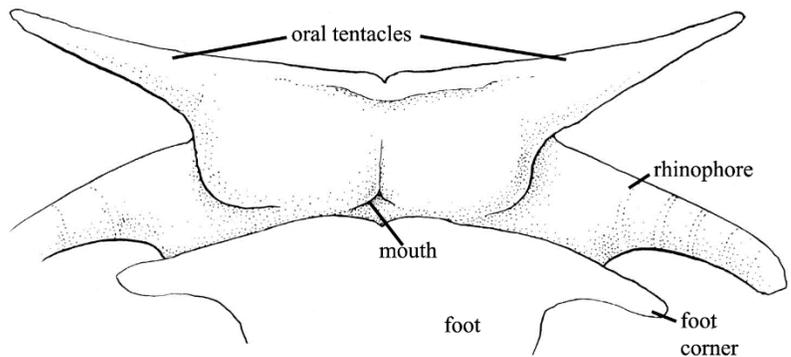
1. Dorsal view (L:50mm) x4:

long oral tentacles; prolonged foot corners; bluish-white line down oral tentacles, around dorsal edge along midline, doubling to enclose orange stripe. Rhinophores weakly annulate; cerata long, white tipped, with orange bands, brown cores, sometimes with white stripe.



2. Anterior, lateral view.

3. Anterior, ventral view.

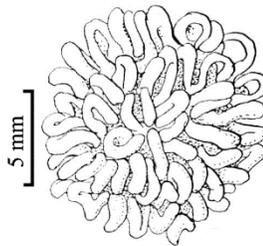


no
branchial
gills

lines
tail



4. Radular tooth:
large middle cusp with
4-6 spines either side
(from Marcus 1961).



5. Egg mass (D:12mm) x3:
sausage-like ribbon of pink capsules
in counter-clockwise coil.

(McDonald and Nybakken 1980). *i.e.* *Onchidoris*, *Triopha*.

Another suborder, Dendronotacea, resemble aeolids, but have sheaths for their rhinophores and a mid-lateral anus. Examples are *Tritonia*, *Tethys*, *Melibe*, and especially *Dendronotus* spp.

The Arminacea are a very diverse group lacking rhinophore sheaths and usually lacking oral tentacles; the anus is anterior. Some have cerata, some do not: *Janolus fuscus* has cerata very like *Hermisenda's* (orange and white tipped), but also has a red cockscomb between the rhinophores, which are colored like the cerata. Cerata begin anterior to the rhinophores and fall off easily; they are found only on the periphery of the dorsum (McDonald and Nybakken 1980). *Janolus* also lacks the blueish lines on the body found on *Hermisenda*. This species was formerly called *Antiopella barbarensis* (Cooper, 1863).

Hermisenda's suborder, Aeolidacea, includes 2 superfamilies, Protoaeolidoidea, with one family, Notaeolidiidae, and Euaeolidoidea, with 21 families. Only a few species from this latter superfamily could be confused with *Hermisenda*:

Fiona pinnata is similar in morphology to *Hermisenda*, but has smooth rhinophores and sail-like flaps on its cerata. The cerata are dense along the margins; a large part of the back is clear (Keen 1971); it has no blue lines or orange spots. Cosmopolitan.

The Coryphellidae have produced foot corners, but not angular ones as in Facelinidae (Keen 1971). Their numerous cerata are clustered and elongate, as in *Hermisenda*. *Coryphella trilineata* has 3 white (not blue) lines on a white body, but there are no orange spots within them. The cerata can look much like *Hermisenda's*, but have cadmium yellow tips. The rhinophores are annulate and colored yellow or orange.

Aeolidia papillosa, the shag rug nudibranch found with anemones, is white with gray to brown spots. It has sharp pedal tentacles like *Hermisenda*, but its cerata begin anterior to the rhinophores and are lanceolate, *i.e.* broad-based and sharp-tipped, not conical as in *Hermisenda*.

Spurillidae (genus *Spurilla*) have rhinophores with quite oblique leaves, and have orange head markings. The cerata of *S. olivae* are quite like *Hermisenda's*: orange, white tipped brown cores. Both this species

and *S. chromosoma* are found only from central California south however (McDonald and Nybakken 1980).

There are 2 other nudibranchs in the family Facelinidae (was Phidianidae (McDonald and Nybakken 1980)), of the genus *Phidiana*; both are found only from central California south: Both *P. hiltoni* (= *pugnax*) and *P. (Emarcusia?) morrowensis* have orange markings on the head and on the rhinophores. These 2 are closely related, but not likely to be confused with each other or with *Hermisenda*.

Several other nudibranchs of diverse families could resemble *Hermisenda* superficially in color, so care must be taken to observe carefully the rhinophores, foot tentacles, and especially the blue/white lines of *Hermisenda*.

Ecological Information

Range—Sitka, Alaska to Baja California (Beeman and Williams 1980).

Local Distribution—Coos Bay: small boat basin, Charleston, seasonally, especially in summer.

Habitat—varied: rocky tidepools as well as floats, mud and sand flats (Beeman and Williams 1980; Goddard 1985); eelgrass beds (Puget Sound); bare rock.

Salinity—collected at 30 ‰ (Coos Bay)

Temperature—annual range 9-18 degrees (Beeman and Williams 1980).

Tidal Level—low intertidal; subtidal down to 35m (Beeman and Williams 1980).

Associates—copepod *Hemicyclops thysanotus* often found on its back (Beeman and Williams 1980). Found on fouling panels regardless of presence of other organisms. Sea pen *Ptilosarcus* (Puget Sound (Birkeland 1974)). Also see "Food".

Quantitative Information

Weight—5-8 grams (Harrigan and Alkon 1978).

Abundance—one of the most common aeolids in northeastern Pacific, especially in middle of range; but its occurrence is temporally variable at any one part of the range (Ricketts and Calvin 1971). Dominant littoral opisthobranch in abundance and geographical distribution, Humboldt Bay, California (Jaekle 1984). Occurs in Puget Sound sea pen beds at densities up to 2-3/m² (Birkeland 1974).

Life History Information

Reproduction—hermaphroditic, but self-fertilization probably unlikely (Harrigan and Alkon 1978). Mating animals and egg masses found all year (Puget Sound) (Beeman and Williams 1980). Eggs on algae or *Zostera* blades. Egg-laying begins when animal is 45 days old, continues until death (in lab) at 128+ days (Harrigan and Alkon 1978). Motile sperm found in 34 mg animals, egg laying by 73 mg wild animals (in lab (Harrigan and Alkon 1978)). Violent lunging and biting behavior once thought to be aggressive only is now known to be part of brief mating sequence (Rutowski 1983); many attempts at copulation unsuccessful. Sperm from one copulation enough to fertilize most eggs in about 3 egg masses (Rutowski 1983).

Growth Rate—obligatory veliger stage of at least 34 days; veligers hatch in 5-6 days in lab at 13-15 °C (Harrigan and Alkon 1978). Metamorphosis occurs when veligers are at least 300 µ and possess eyes, foot and enlarged propodium (Harrigan and Alkon 1978). Veligers can swim.

Longevity—average life span in lab 163 days (35 veliger + 128 day adult): a subannual species (Harrigan and Alkon 1978).

Food—a generalist: carnivore and scavenger. Eats hydroids, particularly in eelgrass; *Tubularia*, *Eudendrium*, *Sarsia* (Goddard 1985). Also small sea anemones, bryozoans, colonial ascidian *Aplidium*, botryllid ascidians, annelids, small crustaceans and clams, dead animals. Will eat other *Hermisenda* (but probably only when other food not available Goddard 1985)). Subtidally in Puget Sound: sea pen *Ptilosarcus* (Birkeland 1974). In Humboldt Co., California, prey include anthomedusae, leptomedusae and chondrophore *Velella velella* (Jaeckl 1984). Veligers crawl on *Obelia*, a probable food (Harrigan and Alkon 1978).

Predators—in rocky areas below Monterey, California, the large opisthobranch *Navanax inermis* (Beeman and Williams 1980). Seastar *Crossaster* (Puget Sound (Birkeland 1974)) prefers *Hermisenda* as summer food. Eggs eaten by sacoglossan *Olea hansineensis* (Crane, 1971).

Behavior—very aggressive toward other nudibranchs and other *Hermisenda*. Head-on “combats” with the latter probably often part of mating sequence (see *Reproduction*). Small *Hermisenda* have a swimming escape

response to seastar predator *Crossaster* (Birkeland 1974).

Bibliography

1. BEEMAN, R. D., and G. C. WILLIAMS. *Chapter 14. Opisthobranchia and Pulmonata: the sea slugs and allies.*, p. 308–354. *In: Intertidal invertebrates of California.* R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, California.
2. BEHRENS, D. W. 1980. Pacific coast nudibranchs : a guide to the opisthobranchs of the northeastern Pacific. Sea Challengers, Los Osos, Calif.
3. BIRKELAND, C. 1974. Interactions between a sea pen and seven of its predators. *Ecological Monographs.* 44:211-232.
4. FARMER, W. M. 1980. Sea-slug gastropods. W.M. Farmer Enterprises, Tempe, AZ.
5. GODDARD, J. H. R. 1985. Personal communication. Oregon Institute of Marine Biology, Charleston, Or.
6. HARRIGAN, J. F., and D. L. ALKON. 1978. Larval rearing, metamorphosis, growth and reproduction of the eolid nudibranch *Hermisenda crassicornis* (eschschooltz, 1831) (gastropoda: opisthobranchia). *The Biological bulletin.* 154:430-9.
7. HURST, A. 1967. The egg masses and veligers of thirty northeast Pacific opisthobranchs. *The Veliger.* 9:255-288.
8. JAECKLE, W. B. 1984. The opisthobranch mollusks of Humboldt County, California. *The Veliger.* 26:207-213.
9. KEEN, A. M. 1971. Sea shells of tropical west America; marine mollusks from Baja California to Peru. Stanford University Press, Stanford.
10. KOZLOFF, E. N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle & London.
11. MACFARLAND, F. M. 1966. Studies of opisthobranchiate mollusks of the Pacific coast of N. America. *California Acad. of Sciences*, [S.I.].
12. MCDONALD, G. R. 1975. Orders

- Sacoglossa and Nudibranchia, p. 522-542. *In*: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
13. MCDONALD, G. R., and J. W. NYBAKKEN. 1980. Guide to the nudibranchs of California : including most species found from Alaska to Oregon. American Malacologists, Melbourne, Fla.
 14. RICKETTS, E. F., and J. CALVIN. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
 15. RUTOWSKI, R. L. 1983. Mating and Egg Mass Production in the Aeolid Nudibranch *Hermissenda crassicornis* (Gastropoda: Opisthobranchia). *Biological Bulletin*. 165:276-285.

Updated 1988

Onchidoris bilamellata

Many-gilled onchidoris nudibranch

Phylum: Mollusca
Class: Gastropoda, Opisthobranchia
Order: Nudibranchia
Family: Onchidoridae

Description

Size—usual length 15 mm (McDonald 1980); this specimen 15.5 mm long, 11 mm wide, 6 mm high. Far northern and Atlantic specimens can reach 30 mm length (Marcus 1961).

Color—translucent brownish-white with irregular dark or rusty brown splotches, sometimes as irregular longitudinal stripes. Commonly a light spot between the dark rhinophores; gills dull white, underside a dull white. "No yellow pigment," but some specimens without brown color (Kozloff 1974a).

Body Shape—doridiform: oval; generally large, with a broad flat foot, thick fleshy mantle and conspicuous double circlet of gills dorsally (figs. 1, 2). Dorsum covered with many large round papillae, becoming smaller at edges. Surface firm. No large processes except rhinophores, gills, papillae.

Rhinophores—a single pair, perfoliate: genus *Onchidoris* (fig. 1). Rhinophores not especially long.

Gills—16-32 (or more: 36 this specimen); uniplanate, almost erect branchial plumes arranged in two semicircles just anterior to anus: species *bilamellata* (McDonald and Nybakken 1978). Gills not completely retractible (Kozloff 1974a) (fig. 1).

Labial Tentacles—none; fused as an oral veil.

Papillae—mushroom-shaped, with protruding spicules (fig. 3).

Eggs—type A (Hurst 1967): a short, stout spiral ribbon attached along one edge (O'Donoghue and O'Donoghue 1922) (fig. 5); Capsules of 1-3 eggs, ribbons of 6,000 eggs (average).

Veliger—shell average length 146.9 x 95 (Hurst 1967) (fig. 6).

Possible Misidentifications

There are other oval dorid nudibranchs of the same general coloration and shape as *Onchidoris*: *Discocordis*, *Anisodoris*, *Archidoris*, and especially *Acanthodoris brunnea* are all found in our area. None of

these has 16-32 single, branchial plumes arranged in the unusual two semicircles. *Acanthodoris brunnea* can be distinguished immediately; by its very long rhinophores and conical papillae (not round ones), and by its but 7 branchial gills.

A pulmonate, resembling a small shell-less limpet, is colored quite like *Onchidoris*: it is *Onchidella borealis*. Close inspection reveals it to have stalked eyes, and only 20-24 papillae dorsally (Morris et al. 1980).

Ecological Information

Range—Aleutian Islands south to Morro Bay, California (McDonald 1980).

Local Distribution—Coos Bay; Pigeon Point.

Habitat—usually found with barnacle *Balanus*; at Pigeon Point on and under rocks; mudflats.

Salinity—collected at 30 ‰ salt.

Temperature—

Tidal Level—intertidal to 250 m (McDonald 1980); collected at mid-intertidal.

Associates—*Balanus*, chiton *Mopalia*, crabs *Hemigrapsus*, *Cancer oregonensis*, gastropods *Tegula*, *Nucella*, sea star *Pisaster ochraceus*, anthozoans *Anthopleura elegantissima*, *A. artemisia*, isopod *Idotea P. wosnesenskii*.

Quantitative Information

Weight—wet: 0.7 gr.

Abundance—"frequent" (McDonald 1980); seasonally common.

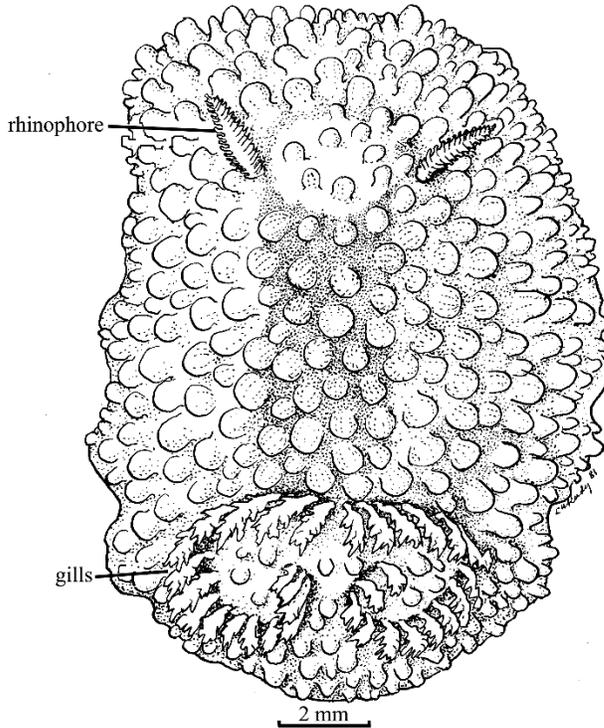
Life History Information

Reproduction—hermaphroditic but not self-fertilizing; internal fertilization. Eggs laid in ribbons during February-March, and October-December (Puget Sound) (Hurst 1967); May to mid-June: British Columbia (O'Donoghue and O'Donoghue 1922).

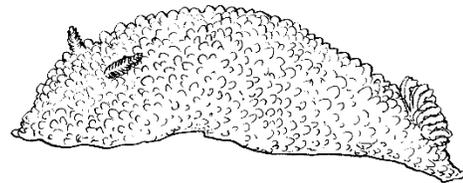
Growth Rate—

Longevity—most opisthobranchs live less than a year (Morris et al. 1980).

Onchidoris bilamellata



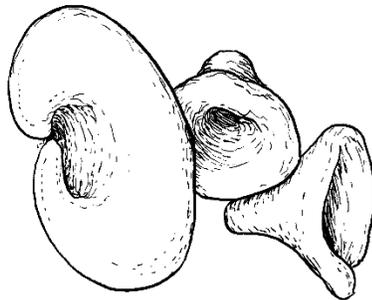
1. *O. bilamellata* (dorsal view) x8:
actual length 15.5 mm; solid oval, dorid nudibranch;
covered with round papilla; posterior double circle
of 16-32 or more gills; bilamellate rhinophores.



2. *O. bilamellata* (lateral view) x5.

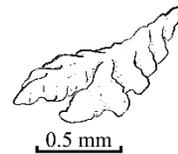


3. Single papilla x40:
spicules protrude.



5. Egg ribbon x2
(O'Donoghue & O'Donoghue, 1922).

4. Single branchial
plume x30:
unipinnate gill.



6. Veliger x250
(Hurst, 1967).

Food—barnacles, mostly *Balanus* (McDonald 1980).

Predators—many opisthobranchs are toxic or bad-tasting; predators are mostly other nudibranchs (Morris et al. 1980).

Behavior—

Bibliography

1. HURST, A. 1967. The egg masses and veligers of thirty northeast Pacific opisthobranchs. *The Veliger*. 9:255-288.
2. KOZLOFF, E.N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle & London.
3. MCDONALD, G.R. 1980. Guide to the nudibranchs of California. American Malacologists, Inc., Melbourne, FL.
4. MCDONALD, G. R., and J. W. NYBAKKEN. 1978. Additional notes on the food of some California nudibranchs with a summary of known food habits of California species. *The Veliger*. 21:110-118.
5. MARCUS, E. 1961. Opisthobranch mollusks from California. *The Veliger*. 3 Supplement.
6. MORRIS, R. H., D. P. ABBOTT, and E. C. HADERLIE. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, California.
7. O'DONOGHUE, C. H., and E. O'DONOGHUE. 1922. Notes on the nudibranchiate mollusca from the Vancouver Island region. *Transactions of the Royal Society of Canada*. 14:131-143.

Updated 1983

Myosotella myosotis

A bristle-bearing ear shell

Phylum: Mollusca
Class: Gastropoda, Pulmonata
Order: Basommatophora
Family: Melampidae
(=Ellobiinae)

Description

Size—to 8 mm; this specimen, 4 mm.

Color—variable: chestnut, purplish or yellowish brown; black with striations. Interior porcelain-like (Carlton and Roth 1975).

Shell Shape—rather olive-like; higher than wide, no spiral ridges; spire pointed, elevated; five or more whorls (fig. 1). Aperture rounded, ear-shaped, about ½ shell length.

Columella—3 folds above anterior end, one weakly developed (fig. 3).

Eyes—at bases of cephalic (and only) tentacles: order Basommatophora (fig. 2) (Carlton and Roth 1975).

Operculum—lacking in pulmonates.

Juveniles—with small hairs on edges of sutures, disappear in adult (fig. 4); juveniles wider than adults (shells) (Hedgepeth 1962).

Possible Misidentifications

Of the other salt marsh gastropods, Littorinidae and Lacunidae are stouter and larger than *Myosotella*, turbinate and without elevated spires. The somewhat similarly shaped *Olivella* sp. is much larger (to 30 mm) and has an anterior canal in its aperture; it lives in clean sand, not in salt marshes (see plate).

Assiminea californica is a tiny (about 3 mm) brown gastropod sometimes found with *M. myosotis*. It resembles *Littorina* in shape, being stout and convex; its inner lip is a small thickened callus, without folds.

The many species of the tiny Opisthobranch *Odostomia* spp. resemble *Myosotella* superficially, but lack columellar folds and a radula. They are parasitic.

None of the preceding snails is closely related to *Myosotella*.

Snails of the subclass Pulmonata, which includes the land snails, have a vascularized mantle cavity serving as a lung, in place of gills. There are no other similar pulmonates known in northwestern salt marshes.

(*Melampus olivaceus* is found farther south) (McLean 1969).

Ecological Information

Range—Puget Sound to Anaheim Bay, California (McLean 1969). Probably introduced from the Atlantic coast in the 19th century (Carlton and Roth 1975). (*Myosotella myosotis* is the Atlantic name; *Phytia setifer* or *myosotis* is a west coast equivalent name used by some authors) (Keen and Coan 1974, Kozloff 1974a).

Local Distribution—Coos Bay: South Slough, many stations (Matthews 1979).

Habitat—*Salicornia* marshes, among debris, mud, crevices of docks, pilings.

Salinity—brackish water: about 16 ‰ seawater; avoids immersion (Matthews 1979). Tolerates all salinities including freshwater; well adapted: an air breather.

Temperature—

Tidal Level—near high tide line (Keen and Coan 1974); at levels which are rarely inundated: it is often the only invertebrate at this high level (Kozloff 1974a). South Slough (Coos Bay): found at + 6.0' MLLW.

Associates—ciliates in mantle cavity (Kozloff 1945); prosobranch gastropods *Assiminea californica*, *Littorina sitkana*, *L. (A.) newcombiana*, *L. scutulata*; pulmonate. *Melampus olivaceus* farther south. Amphipod *Orchestia*, isopods. Plants *Spergularia canadensis*, *Distichlis*, *Carex*.

Quantitative Information

Weight—

Abundance—very common in marshes: often only invertebrate found at its tide level.

Life History Information

Reproduction—hermaphroditic.

Growth Rate—

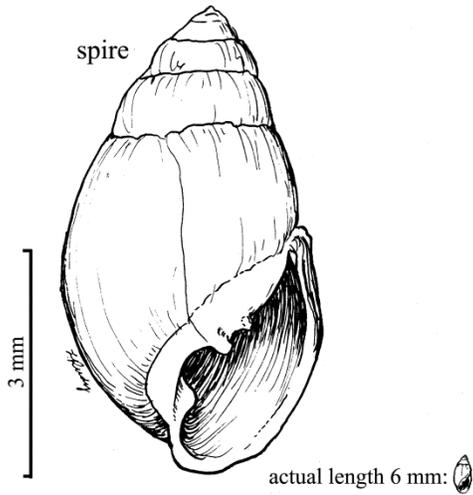
Longevity—

Food—

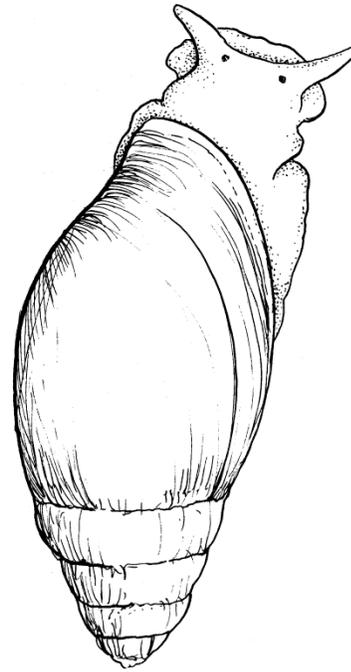
Predators—

Behavior—avoids immersion: an air breather, possessing a lung.

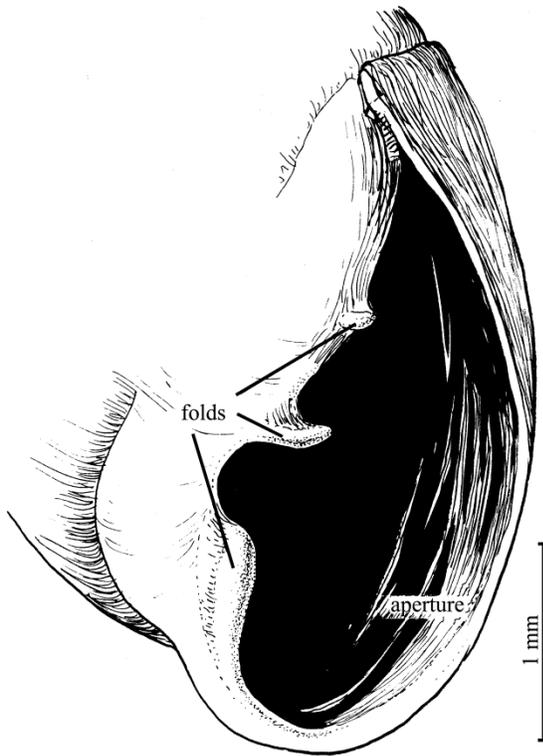
Myosotella myosotis



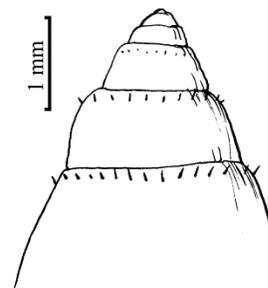
1. *Myosotella myosotis* (anterior view) x12:
higher than wide; 5 or more whorls;
elevated spire; aperture rounded, ear-
shaped and half length of shell.



2. *M. myosotis* (dorsal view) x12:
note eyes at tentacle bases.



3. Columella and aperture (anterior view) x32:
three columellar folds, one weak; no operculum.



4. Juvenile x15:
hairs on sutures.

Bibliography

1. CARLTON, J. T., and B. ROTH. 1975. Phylum Mollusca: Shelled Gastropods, p. 467-514. *In*: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
2. HEDGPETH, J. W. 1962. Introduction to Seashore Life of the San Francisco Bay Region and the Coast of Northern California. California Natural History Guides. 9.
3. KEEN, A. M., and E. COAN. 1974. Marine Molluscan Genera of Western North America: An Illustrated Key. Stanford University Press, Stanford, California.
4. KOZLOFF, E. N. 1945. *Cochliophilus depressus* gen. nov., sp. nov., and *Cochliophilus minor* sp. no. holotrichous ciliates from the mantle cavity of *Phytia setifer* (Cooper). *Biological Bulletin*. 89:95-102.
5. —. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle & London.
6. MATTHEWS, R. 1979. A comparative study of preferred salinities among South Slough snails. Oregon Institute of Marine Biology (University of Oregon).
7. MCLEAN, J. H. 1969. Marine shells of southern California. [Los Angeles] Los Angeles County Museum of Natural History.

Updated 1983

Alderia modesta

A sacoglossan sea slug

Phylum: Mollusca
Class: Gastropoda, Opisthobranchia
Order: Sacoglossa: "shield tongue"
Family: Hermaeidae

Description

Size—to 8 mm long; Coos Bay specimens to 5 mm.

Color—greenish- to yellowish-tan, black markings, base ivory.

Body—'aeolid': changing; an oblong, flat-bottomed form without tentacles or tail (figs. 1, 2).

Rhinophores—reduced, rolled not solid (fig. 1)7; (Kozloff calls these cephalic projections 'dorsolateral tentacles,' not rhinophores) (Kozloff 1974a).

Foot—no parapodia (lateral flaps that could fold over dorsum); foot extends laterally beyond body (Kozloff 1974a).

Cerata—dorsal projections, about 18 (fig. 1), in 2 loose branches on both anterior and posterior halves of dorsum (Kozloff 1974a).

Gills—none.

Eyes—small, black (figs. 1, 2).

Anus—a long tube originating on a medial line, resembling posterior ceratum (McDonald 1975).

Eggs—light yellow, in clear skein (fig. 3).

Possible Misidentifications

Sacoglossans are a little known group of few species and small size, but which can occur in large numbers. *Alderia modesta*, like others of the order, feeds on a specific alga, has a wide distribution, and could probably not be confused with other Opisthobranchs.

Sacoglossans resemble superficially the better known nudibranchs, but unlike them, most do not have a circlet of gills, solid rhinophores, or oral tentacles. (One exception, *Stiliger fuscovittatus*, has solid rhinophores; it is tiny (3 mm), transparent white with reddish brown patterns, and lives in *Polysiphonia*, a red alga.)

Other Sacoglossans with dorsal cerata and rolled rhinophores include, also in the family Hermaeidae

Aplysiosis smithi (= *Hermaeina*), greenish to brownish black with white edges, bulbous cerata, up to 22 mm long; it lives in *Chaetomorpha*, *Rhizoclonium* (its preferred

food), or *Enteromorpha* (Gonor 1961). It has prominent rhinophores and a tail.

Aplysiosis oliviae (= *Hermaea*) has a Y-shaped mahogany line from the rhinophores to the head midline; it is pale yellow with a pink spot behind the eyes.

Hermaea vancouverensis is a small (to 5 mm) brown and white slug, more common in Puget Sound than in the south; its habitat is eelgrass (*Zostera*); its food the diatom *Isthmia* (Williams and Gosliner 1973).

Placida dendritica (= *Hermaea ornata*) has a long, obvious tail, long cerata, and is pale yellow with dark green lines. It is usually on algae *Bryopsis* or *Codium* in the rocky intertidal, and is found in California and Puget Sound (Williams and Gosliner 1973).

Olea hansineensis (family Oleidae) has only about 10 elongate cerata on its posterior dorsum; it is gray, and is found commonly in bays in Puget Sound and probably not in California.

None of these is yellowish tan with small black markings, a tubular anus, and living in *Vaucheria*.

Ecological Information

Range—San Juan Island to Elkhorn Slough, Calif.; Europe (Steinberg 1963).

Local Distribution—Coos Bay: South Slough.

Habitat—found only in mats of alga *Vaucheria* in *Salicornia* marshes.

Salinity—prefers 16-17 ‰ seawater; cannot survive in normal seawater or fresh water (Hyman 1967), although eggs develop in either seawater or brackish water. Cerata pulsation rate varies with salinity (Hyman 1967).

Temperature—

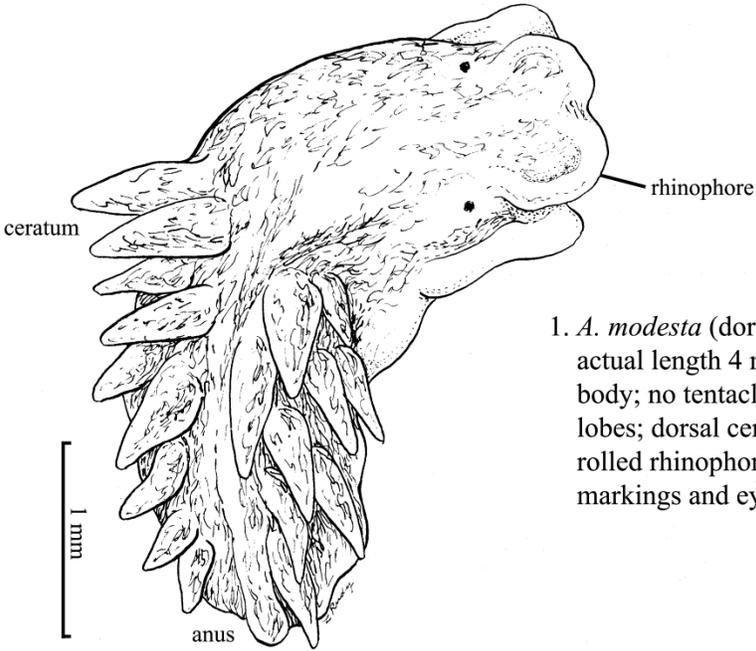
Tidal Level—at higher levels of marsh (Coos Bay): about 4.0'.

Associates—insects; alga *Vaucheria*.

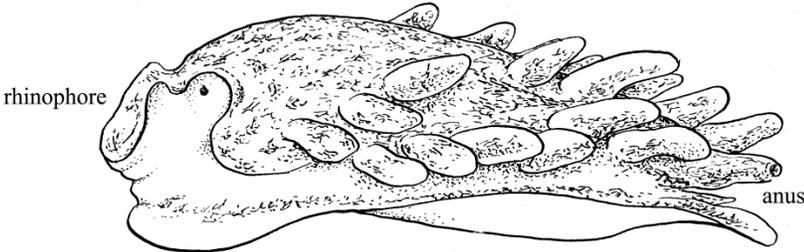
Quantitative Information

Weight—

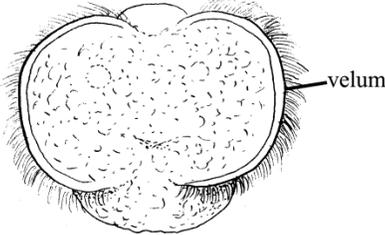
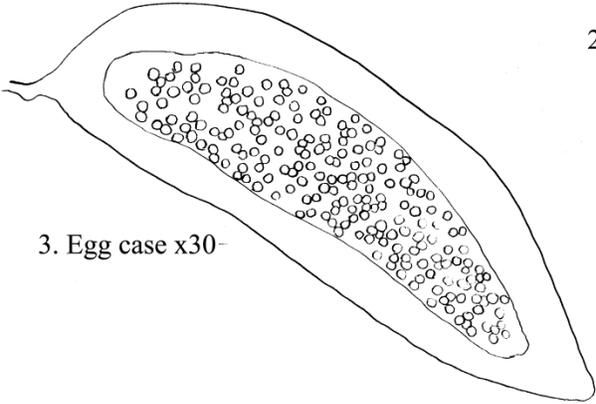
Alderia modesta



1. *A. modesta* (dorsal view) x30:
 actual length 4 mm; oblong, changeable
 body; no tentacles, tail, or parapodial
 lobes; dorsal cerata; anal tube; small
 rolled rhinophores; light tan, black
 markings and eyes.



2. *A. modesta* (lateral view)



4. 2-day veliger

Abundance—common in its particular microhabitat, *Vaucheria* (McDonald 1975).

Life History Information

Reproduction—hermaphroditic; eggs laid in September, Coos Bay (this specimen).

Growth Rate—to early veliger two days in lab (this specimen).

Longevity—

Food—alga *Vaucheria*, exclusively.

Predators—some sacoglossans emit nasty repellents (Hyman 1967).

Behavior—

Bibliography

1. GONOR, J. J. 1961. Observations on the biology of *Hermaeina smithi*, a sacoglossan opisthobranch from the west coast of North America. *The Veliger*. 4:85-98.
2. HYMAN, L. H. 1967. *The invertebrates: mollusca*. McGraw-Hill, New York.
3. KOZLOFF, E. N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle & London.
4. MCDONALD, G. R. 1975. Orders Sacoglossa and Nudibranchia, p. 522-542. *In*: Light's manual; intertidal invertebrates of the central California coast. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
5. STEINBERG, J. E. 1963. Notes on the Opisthobranchs of the west coast of North America. *The Veliger*. 6:68-73.
6. WILLIAMS, G. C., and T. M. GOSLINER. 1973. Range extensions of four sacoglossan opisthobranchs from the coasts of California and the Gulf of California. *The Veliger*. 16:112-116.

Updated 1983

Aplysiopsis enteromorphae

Smith's unwashed-looking sacoglossan

Phylum: Mollusca
Class: Gastropoda
Order: Sacoglossa
Family: Hermaeidae

Description

Size—to 25 mm long (Behrens 1980); most are 10 mm (Goddard 1985), some to 15 mm (Gonor 1961). Illustrated specimen (Coos Bay) 15 mm long.

Color—yellowish white, with greenish black patches; animal can be almost black: much local variation (Gonor 1961). Head uniform in color, dorsal cerata white or yellow tipped; rhinophores uniform in color, not veined.

Body—"aeolid", oblong, flat bottomed; no oral tentacles or parapodial lobes, but with prominent tail (fig. 1). No circler of external gills: order Sacoglossa.

Rhinophores—prominent; rolled, not solid: order Sacoglossa (fig. 1). (Basal part rolled, distal part simple (Kozloff 1974a)). Color uniform, without system of lines.

Foot—no parapodial lobes (which fold over body in some species); foot extends to form tail (Gonor 1961).

Cerata—(singular = ceras): dorsal processes: spindle shaped, inflated, white tipped; 8 - 15 rows of 2 to 4 each row (Gonor 1961) (fig. 1).

Gills—none: order Sacoglossa.

Eyes—black, small, but conspicuous; deep set, at bases of rhinophores (fig. 1).

Genital Openings—2, on right behind rhinophore (fig. 1).

Anus—slightly raised, near 2nd and 3rd cerata, with black spot and renal opening near it (Gonor 1961) (fig. 1). Anus on midline at "shoulders" not on a long tube.

Eggs—yellow to white, in "C" shaped string 14 mm x 15 mm; eggs become paler as they develop (Goddard 1984; Gonor 1961). Eggs average 66 µ in diameter (fig. 3).

Possible Misidentifications

Sacoglossans differ from most Nudibranchia in their lack of a circler of gills, and by their rolled, rather than solid rhinophores. They also lack oral tentacles, and have a uniseriate radula (Thompson 1976). Sacoglossans are herbivorous. There are other sacoglossans with dorsal cerata and

rolled rhinophores, in 3 families - Alderiidae, Hermaeidae, and Stiligeridae. (The 1st 2 have been removed from the 3rd Kozloff 1974a)).

Among the Alderiidae, *Alderia modesta* (which see) has reduced rhinophores and an anus on a long posterior tube like a ceras. It lives in *Salicornia* marshes.

In the family Hermaeidae is *Hermaea vancouverensis*, a bay form like *Aplysiopsis*, but very small (5 mm). It has a triangular brown patch anterior to the rhinophores, and a brown collar anterior to the cerata. Its habitat is in the sea grass *Zostera*.

The Stiligeridae are represented locally by at least 3 species:

Placida dendritica (= *Hermaea ornata*) has long rhinophores and an elongate tail (like *Aplysiopsis*), but its cerata are long and not lumpy, and its ground color is pale yellow with a distinct veining of olive. It is quite small (to 8 mm), and is often found in the green algae *Bryopsis* and *Codium* in the rocky intertidal.

Olea hansineensis (formerly in Oleidae) is greenish brown. It has only 10 or fewer white tipped cerata; its rhinophores are short.

Stiliger fuscovittatus differs from most sacoglossans in having solid simple rhinophores; it is small (to 3 mm) and whitish, with rust markings. It lives in the red alga *Polysiphonia*.

In the genus *Aplysiopsis* is *A. oliviae*, a rare and probably more southern species than *A. enteromorphae*. It is up to 10 mm long, and has a Y-shaped dorsal mahogany line running back from the rhinophores.

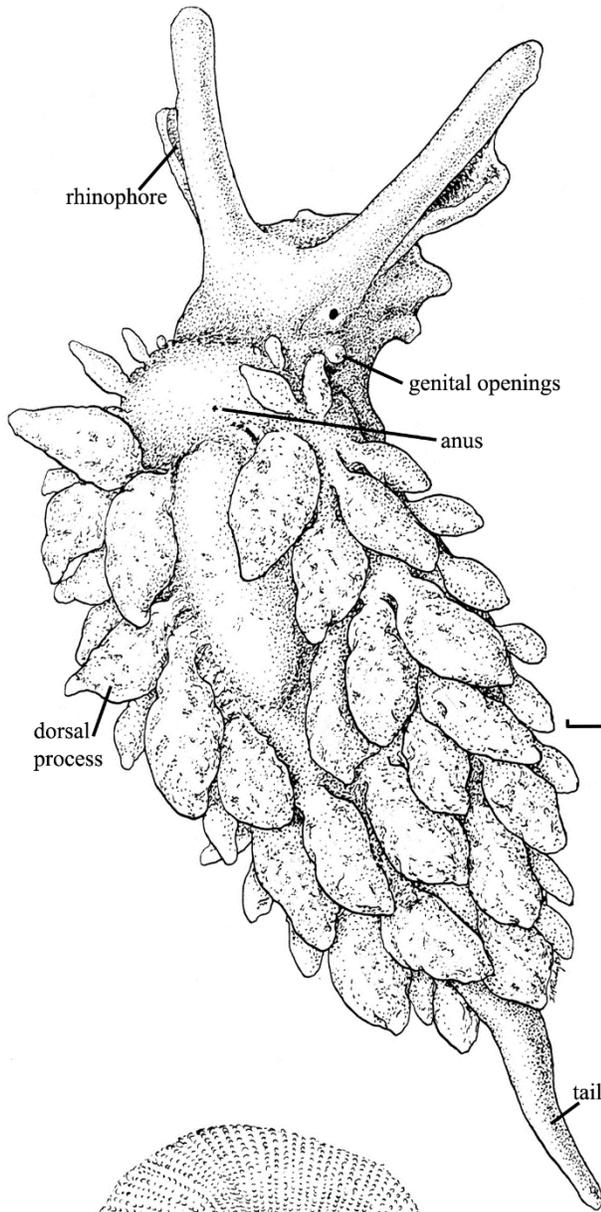
Ecological Information

Range—San Juan Island, Washington to San Diego, California; also in Gulf of California (Behrens 1980).

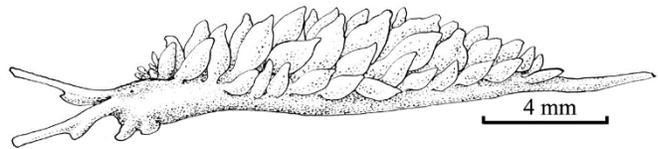
Local Distribution—Coos Bay: South Slough, in Metcalf Preserve.

Habitat—Sacoglossans are typically restricted to certain algae species (Gonor 1961; Thompson 1976). In bays *Aplysiopsis* is commonly found on the green filamentous algae *Rhizoclonium* and *Enteromorpha*. It also likes quiet, shallow mud-bottomed bays

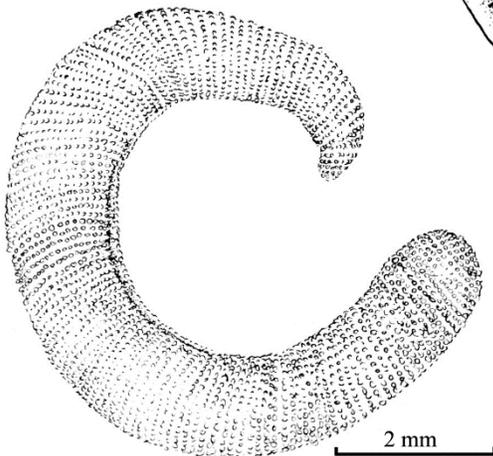
Aplysiopsis enteromorphae



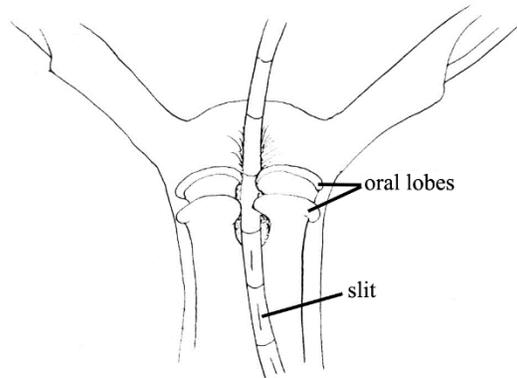
1. *Aplysiopsis enteromorphae* (L: 15mm) x12: dolioliform, no tentacles or gills; large, rolled rhinophores; yellowish white with greenish black patches; dorsal processes inflated, lumpy, white-tipped; no parapodial lobes but a prominent tail.



2. Lateral view x6.



3. Egg string x12: actual size 14 x 1.5mm string "C" shaped; pale yellow eggs 66 μ m in diameter.



4. Head, feeding animal (ventral view): oral lobes grasp stem; radular tooth (within mouth); slits filamentous algal cells (from Gonor 1961).

which have *Zostera* at low tide level and bare mudflats above (San Juan Island). In Coos Bay it is found on bare mudflats near *Enteromorpha* beds. Also found seasonally on green algae *Cladophora* and *Chaetomorpha* in high to mid intertidal pools on open coast rocky shores, as well as in kelp holdfasts (Goddard 1984; Goddard 1985; Keen and Coan 1974).

Salinity—collected at 30 ‰

Temperature—10-15 °C.

Tidal Level—on San Juan Island, found at 0.0 tide level; in Coos Bay at +5.0 ft. MLLW. Intertidal to 10 m subtidally (Keen and Coan 1974).

Associates—in Coos Bay, amphipods *Ampithoe valida*, *Grandidierella japonica*, alga *Enteromorpha*.

Quantitative Information

Weight—

Abundance—probably the most abundant sacoglossan of this coast (Goddard 1985; Gonor 1961) seasonally common (Goddard 1984; Goddard 1985; Steinberg 1963).

Life History Information Reproduction—hermaphroditic; (illustrated) eggs found July (Coos Bay). Lays eggs on *Enteromorpha* strands continuously in lab; larvae emerge as free swimming veligers and apparently have long planktonic feeding phase (Gonor 1961). Embryonic period 7 days at 15-17 °C.; larvae without eyespots at hatching; newly hatched veligers have shell about 113 μ long (Goddard 1984).

Growth Rate—

Longevity—

Food—prefers *Rhizoclonium*, *Urospora*; rejects *Enteromorpha* (Gonor 1961). Feeds by slitting each filament cell with a radula tooth, then moving on to next cell (Gonor 1961) (fig. 4).

Predators—

Behavior—some sacoglossans emit unpleasant repellants from cerata to repel predators (Thompson 1976).

Bibliography

1. BEHRENS, D. W. 1980. Pacific coast nudibranchs : a guide to the opisthobranchs of the northeastern Pacific. Sea Challengers, Los Osos, Calif.

2. GODDARD, J. H. R. 1984. The opisthobranchs of Cape Arago, Oregon, with notes on their biology and a summary of benthic opisthobranchs known from Oregon. *Veliger*. 27:143-163.
3. ——. 1985. Personal communication. Oregon Institute of Marine Biology, Charleston, Or.
4. GONOR, J. J. 1961. Observations on the biology of *Hermaeina smithi*, a sacoglossan opisthobranch from the west coast of North America. *The Veliger*. 4:85-98.
5. KEEN, A. M., and E. COAN. 1974. Marine Molluscan Genera of Western North America: An Illustrated Key. Stanford University Press, Stanford, California.
6. KOZLOFF, E. N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle & London.
7. STEINBERG, J. E. 1963. Notes on the opisthobranchs of the west coast of North America. *The Veliger*. 6:68-73.
8. THOMPSON, T. E. 1976. Biology of opisthobranch molluscs. Ray Society, London.

Updated 1988

Hiatella arctica

The nestling or Arctic saxicave, little gaper, red nose

Phylum: Mollusca
Class: Bivalvia
Order: Veneroida
Family: Hiatellidae

Taxonomy: There are many synonyms for *H. arctica* due to the potentially cosmopolitan distribution of this species. Research by Strauch (1968) and Beu (1969) synonymized all *Hiatella* species worldwide (except *H. australis* from southern Australia) as *H. arctica* (Beu 1969). Commonly seen synonyms include *Saxicava arctica*, *H. pholadis*, and *H. solida*. Due to the extensive synonymizations, it is possible that there are actually two species currently under the name *H. arctica*, locally (Coan and Valentich-Scott 2007).

Description

Size: Individuals to 50–76 mm in length (Kozloff 1993). The illustrated specimen (from Coos Bay) is 38 mm in length (Quayle 1970).

Color: Exterior is white, chalky, granular, and with tan, thin, and ragged periostracum (*Hiatella*, Keen and Coan 1974). The interior is porcelain-like and white (*Hiatellidae*, Hunter 1949). Periostracum is light brown or tan.

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). The Veneroida is a large and diverse bivalve heterodont order that is characterized by well-developed hinge teeth. There are 22 local families, and members of the Hiatellidae are characterized by a pallial line that is divided into patches (see Plate 395D, Coan and Valentich-Scott 2007) (Fig. 3).

Body: A nestling species with a thin shell (see Fig. 257, Kozloff 1993).

Color:

Interior: Ligament is external (Figs. 2–3) in members of the family *Hiatellidae* (Coan and Carlton 1975). This primary ligament initially forms at the shell posterior in newly metamorphosed juveniles before moving to the middle of the shell (Flyachinskaya and Lezin 2008).

Exterior:

Byssus: These attachment threads are present in nestling specimens, but not in boring ones (e.g., *H. pholadis*). Adult attach with byssal threads and can also bore into rock (Coan and Valentich-Scott 2007). A single, long byssal thread produced by post-larval clams allows them to be moved by weak water currents (see **Juvenile**) (Haderlie 1980), in a process called thread drifting (see *Macoma balthica*, *Nutricola tantilla*, descriptions in this guide).

Gills:

Shell: (For amino acid shell composition see Brigham 1983.) Right valve slightly larger than the left (Khalaman 2005) (Fig. 2).

Interior: Pallial line is faint and broken into discontinuous scars (Fig. 3) (*Hiatellidae*, Coan and Valentich-Scott 2007), unlike *Entodesma navicula* (see description in this guide). Adductor muscle scars are approximately equal in size, but not shape. There is no pallial sinus (Kozloff 1974).

Exterior: The shape is highly variable due to their nestling habit. Right and left valves are equal, oblong, and gaping. The posterior is broader and more square than the anterior end, which is broadly truncated (Fig. 1). Elongate, boring specimens have been reported as *H. pholadis* (Coan and Carlton 1975) (Fig. 1a). Shell sculpture is concentric only and the periostracum is light tan and thin (Figs. 1, 2) (*Hiatella*, Keen and Coan 1974).

Hinge: Adult specimens are without (or very worn) hinge teeth (Fig. 3). However, young clams have 1–2 weak, peg-like cardinal teeth. Umbones are depressed, nearer anterior end than middle and do not touch one other (Fig. 2).

Eyes:

Foot:

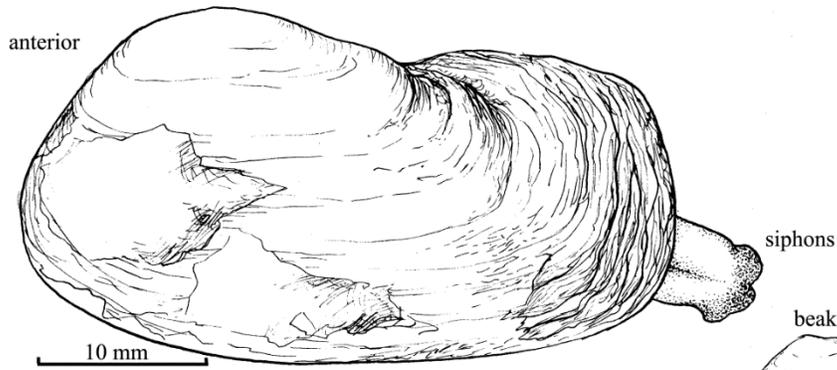
Siphons: Siphons are fused and with crimson siphon tips (Fig. 1) (Kozloff 1993).

Burrow:

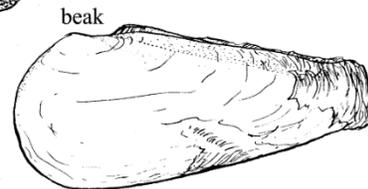
Possible Misidentifications

Three bivalve families including the Lyonisiidae, Hiatellidae, and Thraciidae are characterized by their lack of dorsal margin

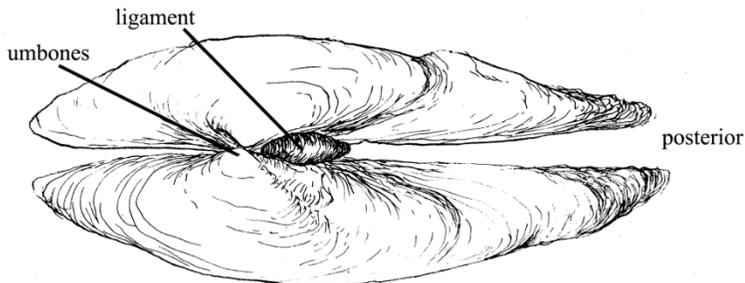
Hiatella arctica



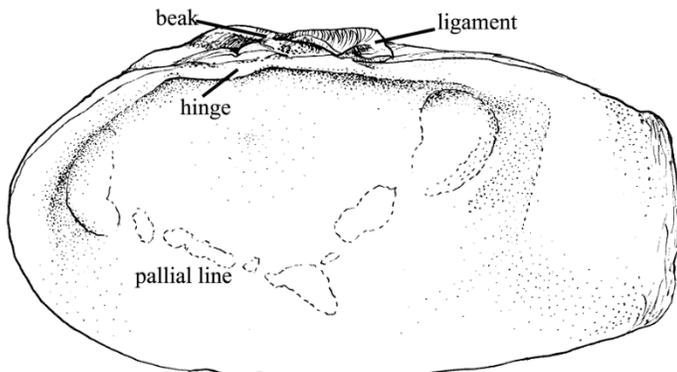
1. *Hiatella arctica*, exterior, left valve (L:38mm) x3:
shell oblong, distorted; posterior truncate, beaks nearer
anterior end than middle; concentric striations on rough,
white surface, thin tan periostracum.



1a. *H. pholadis*, left valve x2:
elongate; beaks near anterior end.



2. (Dorsal view): umbones depressed, not touching; ligament
external, posterior gaping.



3. Interior, right valve: white, porcelain-like; hinge without
teeth; ligament external; pallial line broken into scars.

ears or projecting teeth or chondrophores, and two adductor muscles. In thraciids, the ligament can be both internal and external and the pallial line is continuous; in hiatellids the ligament is always external and the pallial line is broken into patches (see below). On the other hand, in the lyonisiids (e.g., see *Entodesma navicula* in this guide) the pallial line is continuous, as in thraciids, but the ligament is always internal, unlike thraciid species (Coan and Valentich-Scott 2007).

Burrowing and nestling clams, of which there are many genera, can be difficult to separate by shell shape as their nestling habits tend to produce a varied shell shape. Useful characteristics for differentiating species include the hinge teeth, pallial line, and siphons. Most Pholadidae can be distinguished by their two distinct shell sections (see *Penitella penita*, *Zirfaea pilsbryi* in this guide). All pholads have file-like denticulations and (except for *Netastoma*) an internal myophore.

There are only two local species reported in the family Hiatellidae: *Panopea abrupta* and *Hiatella arctica*. *Panopea abrupta* tends to be larger (up to 200 mm in length) than *H. arctica* and have a continuous pallial line, not broken into patches like in *H. arctica*. *Panopea abrupta*, also known as the geoduck, is a very deep burrower with long siphons (up to several feet) in soft sediments. It has one cardinal tooth in either hinge and is rarely found in Oregon. Also, *Saxicavella pacifica*, a small offshore species in soft sediments is reported (Coan and Valentich-Scott 2007).

Entodesma navicula is probably most likely to be confused with *H. arctica*, as it is of a comparable size, shape, and habitat. *Entodesma navicula* has a dark, rough periostracum, not a pale, thin one, an external ligament (like *H. arctica*), and short, fused siphons, but without red tips. Inside the shell is very pink and pearly. *Entodesma navicula* has no hinge teeth, but does have a large internal ligament and its pallial line is continuous.

Other bivalves that can be easily confused with *H. arctica* include *Protothaca staminea*, *Petricola carditoides*, *Platyodon cancellatus*, and *Cryptomya californica*. The venerid clam *Protothaca staminea*, like *H. arctica*, is white with an external ligament, and

can be found nestling in old pholad burrows. It has radial as well as concentric striations, however, and interiorly has three cardinal hinge teeth and a strong pallial line and sinus. *Petricola carditoides* is a nestling clam which has an external ligament and a chalky white shell, as in *H. arctica*. It has 2–3 hinge teeth in the adult, not just in the juveniles. *Petricola carditoides* also has purple-tipped siphons, not crimson, and its shell has some radial sculpture. The myid clam *Platyodon cancellatus* is a white borer with a heavy shell with fine, almost lamellar concentric exterior sculpture. Inside it has a chondrophore and tooth in its hinges, and a well-developed, deep pallial sinus. *Cryptomya californica*, also a myid clam, can nestle among rocks, although its usual habitat is sand or mud. It is small (to 30 mm), thin-shelled and has a chondrophore. Interiorly it has an entire pallial line, and an inconspicuous pallial sinus (Coan and Carlton 1975).

Ecological Information

Range: Type region is the Arctic coast of Norway (Keen 1971) A circumpolar species with known range from Arctic Ocean to Panama (Oldroyd 1924). Range is certainly influenced by many human introductions (Beu 1971; Narchi 1973; Russell-Hunter 1949; Yonge 197), and potentially includes two species as a result (Coan and Valentich-Scott 2007) (see **Taxonomy**). In Cow Head, Newfoundland, radiocarbon age of *H. arctica* fossils embedded in rock were approximately 8,250 years BP (Brookes and Stevens 1984). The genus *Hiatella* is widespread in polar latitudes dating to 150 million years ago (Laakkonen et al. 2015). A recent molecular analysis of over 350 specimens using three gene regions suggests cryptic speciation rather than widespread distribution, including at least 13 different putative species, several of them living sympatrically (Laakkonen et al. 2015). These authors found several distinct lineages within the northeast Pacific (see Laakkonen et al. 2015).

Local Distribution: Local distribution in Coos Bay including Pigeon Point.

Habitat: Individuals nestle in old pholad burrows or bore into smooth, soft, homogenous rocks. They are also found in mussel (e.g., *Mytilus*) clumps, on pilings, and on open coasts within algal holdfasts. On hard surfaces and within crevices, individuals

attach byssally (Hunter 1949). Prefers sheltered locations or being covered by other organisms (Khalaman 2005).

Salinity: Occurs in Coos Bay as well as more saline parts of estuary, and individuals have been collected at salinities of 30. Heart rates 10 to 16 beats per minute at normal salinities but drops dramatically in response to a change in salinity, returning to normal after 2–7 days (Bakhmet et al. 2012).

Temperature: Temperature may affect shell growth and structure (see **Larva**) leading Lezin et al. (2015) to question the relevance of shell structure as taxonomic characters and for estimation of sea surface temperature (but see Strauch 1968, 1971). Shell shape is also certainly affected by the nestling habits of individuals (see Rowland and Hopkins 1971).

Tidal Level: Intertidal to 120 m deep, but also low or subtidal when attached (with byssus) under rocks, on floats or pilings (Morgan and Allen 1976; Morton 1987; Yonge 1952, 1976; Coan and Valentich-Scott 2007). The highest abundance of individuals (57 per square meter) was observed at 20-meter depths in the Young Sound, northeast Greenland (Sejr et al. 2002).

Associates: Associates include other nestling and boring molluscs (e.g., *Entodesma navicula*, *Penitella penita*, *Zirfaea pilsbryi*). A potential competitor affecting settlement of *Pecten maximus*, the great scallop in the Bay of Brest in France (Chauvard et al. 1996). *Hiatella arctica* is a facultative epibiont of the crab *Hemigrapsus sanguineus* in Japan (Isaeva et al. 2001). Competes with and often associated with *Mytilus edulis* fouling communities (Khalaman 2005). Also co-occurs with the solitary ascidian *Styela rustica*, in the White Sea (Khalaman 2007).

Abundance: Not common locally, however, *H. arctica* is the dominant byssal bivalve in the arctic and boreal regions (Coan and Valentich-Scott 2007). Along with *Mytilus edulis*, *H. arctica* was the most abundant bivalves in Eyjafjordur, North Iceland, with newly metamorphosed spat observed on settlement plates throughout the year (Garcia et al. 2008). Density reached approximately 815 individuals per meter in the White Sea (Khalaman 2005).

Life-History Information

Reproduction: Spawning occurs from mid June through September and veliger larvae are present through November (White Sea, Russia, Flyachinskaya and Lesin 2006). The early development is apparently very similar to *Mytilus edulis* (see description in this guide), which was described by Malakhov and Medvedeva (1985).

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the “D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone (see Fig. 1, Caddy 1969). Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig. 1, Caddy 1969; Kabat and O’Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001). Larval development was described by Flyachinskaya and Lesin (2006) where straight hinge larvae were 120 µm, umbo were 160 µm, early pediveligers were 220 µm, pediveligers were 310 µm and grew to 400 µm pre-metamorphosis and were 750 µm post-metamorphosis (see Fig. 3, Flyachinskaya and Lesin 2006). The shell is yellowish pink when early in development and changes to a darker (dirtier) yellow with pink margins. Veliger larvae of *H. arctica* have a distinctly triangular shell and there are two distinct posterior dorsal spines on the dissoconch in newly metamorphosed *H. arctica* (see Fig. 3F, Flyachinskaya and Lezin 2006). These spines are lost in adulthood (Flyachinskaya and Lezin 2008). Settlement was observed throughout the year in Eyjafjordur, Iceland with peaks in abundance of primary (<1mm) settlers in September. Lezin et al. (2015) found that larvae and juveniles raised at 12°C formed ridges and

spines on the shell posterior. However, they developed fewer or inconspicuous spines at lower temperatures (e.g., 5°C) (Lezin et al. 2015). Wild-caught planktonic larvae measured up to 380 µm in the North Sea and had a tough shell, a conspicuous pallial line, and concentric ridges that become more pronounced and widely spaced with distance from the umbo (Rees 1950).

Juvenile: Like other bivalve species (e.g. *Mytilus edulis*, *Macoma balthica*), post-larval (i.e., juvenile) *H. arctica* may exploit two dispersal periods. The initial larval dispersal and settlement into the benthos, is followed by potential dispersal from the benthos by thread drifting on water currents via mucous threads by juveniles (i.e., “thread drifting”, Martel and Chia 1991).

Longevity: Age was estimated for individuals in the Young Sound, northeast Greenland by counting growth rings (a method validated by Sejr et al. 200b); the oldest individuals were estimated to be 126 years old (Sejr et al. 2002a).

Growth Rate: Mean growth rate was estimated to be 0.14 mm per year in northeast Greenland (Sejr et al. 2002a).

Food: A suspension feeder. Filtration rates were 1.4 x 10⁻² liters per hour per gram wet weight (*Phaeodactylum tricornutum*, 15°C) and increases up to temperatures of 17°C before decreasing above 25°C (Ali 1970), at high temperatures *H. arctica* close their valves completely (Petersen et al. 2003). Clearance rates for individuals at varying temperatures were recorded by Petersen et al. (2003) for individuals collected in the Arctic (Young Sound, northeast Greenland) and temperate waters (Tjarno, Sweden) (see Table 1, Petersen et al. 2003) and averages being approximately 23.4 and 27.4 ml per minute per gram body weight those from the Arctic and Sweden, respectively (Petersen et al. 2003). Clearance rates and assimilation efficiency (how much food is metabolized) of *Rhodomonas baltica* decreases with increasing food concentration (Sejr et al. 2004). Sejr et al. (2004) found that individuals grow to annual observed growth in the wild in three weeks at optimal feeding conditions in the laboratory and suggest that food is limiting in wild populations.

Predators: Toothed snails (e.g., *Nucella* spp.) can prey on small nestling clams like *H. arctica*.

Behavior: Individuals bore mechanically and without the aid of chemical compounds (Hunter 1949).

Bibliography

1. ALI, R. M. 1970. Influence of suspension density and temperature on filtration rate of *Hiatella arctica*. *Marine Biology*. 6:291-302.
2. BAKHMET, I. N., A. J. KOMENDANTOV, and A. O. SMUROV. 2012. Effect of salinity change on cardiac activity in *Hiatella arctica* and *Modiolus modiolus*, in the White Sea. *Polar Biology*. 35:143-148.
3. BEU, A. G. 1971. New light on variation and taxonomy of bivalve *Hiatella*. *New Zealand Journal of Geology and Geophysics*. 14:64-66.
4. BRIGHAM, J. K. 1983. Intrashell variations in amino acid concentrations and isoleucine epimerization ratios in fossil *Hiatella arctica*. *Geology*. 11:509-513.
5. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
6. BROOKES, I. A., and R. K. STEVENS. 1985. Radiocarbon age of rock boring *Hiatella arctica* (Linne) and postglacial sea level change at Cow-Head, Newfoundland. *Canadian Journal of Earth Sciences*. 22:136-140.
7. CHAUVAUD, L., G. THOUZEAU, and J. GRALL. 1996. Experimental collection of great scallop postlarvae and other benthic species in the Bay of Brest: Settlement patterns in relation to spatio-temporal variability of environmental factors. *Aquaculture International*. 4:263-288.
8. COAN, E. V., and J. T. CARLTON. 1975. Phylum Mollusca: Bivalvia, p. 543-578. *In: Light's manual; intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.

9. COAN, E. V., and P. VALENTICH-SCOTT. 2007. *Bivalvia*, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
10. FLYACHINSKAYA, L. P., and P. A. LESIN. 2006. Using 3D reconstruction method in the investigations of bivalvia larval development (by the example of *Hiatella arctica* L.). *Trudy Zoologicheskogo Instituta*. 310:45-50.
11. FLYACHINSKAYA, L. P., and P. A. LEZIN. 2008. Larval and juvenile shell development in the White Sea bivalve *Hiatella arctica* (Linnaeus, 1767). *Zoologiya Bespozvonochnykh*. 5:39-46.
12. GARCIA, E. G., G. G. THORARINSDOTTIR, and S. A. RAGNARSSON. 2003. Settlement of bivalve spat on artificial collectors in Eyjafjordur, North Iceland. *Hydrobiologia*. 503:131-141.
13. HADERLIE, E. C., and D. P. ABBOTT. 1980. *Bivalvia: the clams and allies*, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
14. HUNTER, W. R. 1949. The structure and behavior of *Hiatella gallicana* (Lamarck) and *H. artica* (L.) with special reference to the boring point. *Proceedings of the Royal Society of Edinburgh, Series B*. 63:271-289.
15. ISAEVA, V., V. KULIKOVA, and I. KASYANOV. 2001. Bivalve molluscs, *Mytilus trossulus* and *Hiatella arctica*, as facultative epibionts of the crab, *Hemigrapsus sanguineus*, infested by the rhizocephalan, *Sacculina polygenea*. *Journal of the Marine Biological Association of the United Kingdom*. 81:891-892.
16. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
17. KEEN, A. M. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. Stanford University Press, Stanford, CA.
18. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
19. KHALAMAN, V. V. 2005. Testing the hypothesis of tolerance strategies in *Hiatella arctica* L. (Mollusca: Bivalvia). *Helgoland Marine Research*. 59:187-195.
20. KHALAMAN, V. V., and A. Y. KOMENDANTOV. 2007. Mutual influence on survival and growth rate in fouling organisms *Mytilus edulis*, *Styela rustica* and *Hiatella arctica* from the White Sea. *Biologiya Morya*. 33:176-181.
21. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
22. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
23. LAAKKONEN, H. M., P. STRELKOV, and R. VAINOLA. 2015. Molecular lineage diversity and inter-oceanic biogeographical history in *Hiatella* (Mollusca, Bivalvia). *Zoologica Scripta*. 44:383-402.
24. LEZIN, P., and L. FLYACHINSKAYA. 2015. Shell sculpture formation in bivalves of the genus *Hiatella* under different temperature conditions. *Journal of the Marine Biological Association of the United Kingdom*. 95:1621-1627.
25. MALAKHOV, V. V., and L. A. MEDVEDEVA. 1985. Embryonic and early larval development in the bivalve *Mytilus edulis* (Mytilida, Mytilidae). *Zoologicheskyy Zhurnal*. 64:1808-1815.
26. MARTEL, A., and F. S. CHIA. 1991. Drifting and dispersal of small bivalves and gastropods with direct development. *Journal of Experimental Marine Biology and Ecology*. 150:131-147.

27. OLDROYD, I. S. 1924. Marine shells of Puget Sound and vicinity. University of Washington Press, Seattle.
28. PETERSEN, J. K., M. K. SEJR, and J. E. N. LARSEN. 2003. Clearance rates in the arctic bivalves *Hiatella arctica* and *Mya* sp. *Polar Biology*. 26:334-341.
29. QUAYLE, D. B. 1970. The intertidal bivalves of British Columbia. British Columbia Provincial Museum, Victoria, BC, Canada.
30. REES, C. B. 1950. The identification and classification of lamellibranch larvae. *Hull Bulletins of Marine Ecology*. 3:73-103.
31. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
32. —. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
33. ROWLAND, R. W., and D. M. HOPKINS. 1971. Comments on use of *Hiatella arctica* for determining Cenozoic sea temperatures. *Palaeogeography Palaeoclimatology Palaeoecology*. 9:59-61.
34. SEJR, M. K., K. T. JENSEN, and S. RYSGAARD. 2002a. Annual growth bands in the bivalve *Hiatella arctica* validated by a mark-recapture study in N.E. Greenland. *Polar Biology*. 25:794-796.
35. SEJR, M. K., J. K. PETERSEN, K. T. JENSEN, and S. RYSGAARD. 2004. Effects of food concentration on clearance rate and energy budget of the Arctic bivalve *Hiatella arctica* (L) at subzero temperature. *Journal of Experimental Marine Biology and Ecology*. 311:171-183.
36. SEJR, M. K., M. K. SAND, K. T. JENSEN, J. K. PETERSEN, P. B. CHRISTENSEN, and S. RYSGAARD. 2002b. Growth and production of *Hiatella arctica* (Bivalvia) in a high-arctic fjord (Young Sound, Northeast Greenland). *Marine Ecology Progress Series*. 244:163-169.
37. STRAUCH, F. 1968. Determination of Cenozoic sea-temperatures using *Hiatella arctica* (Linne). *Palaeogeography Palaeoclimatology Palaeoecology*. 5:213-233.
38. —. 1971. Some remarks on *Hiatella* as an indicator of sea temperatures. *Palaeogeography Palaeoclimatology Palaeoecology*. 9:62-64.

Updated 2016

Cryptomya californica

False Mya

Phylum: Mollusca
Class: Bivalvia; Heterodonta
Order: Myoida
Family: Myidae

Taxonomy: *Sphenia californica* is the original name given to *Cryptomya californica* (Keen 1966; Coan 1999; Coan and Valentich-Scott 2012). Although *C. californica* is almost exclusively used currently, the taxonomy of this species includes many synonyms (e.g., *Cryptomya kamtschatica*, *C. magna*, *C. oregonensis*, *C. quadrata*, *C. washingtoniana*, *Macoma kerica*, *Mya inopia*, *M. mindorensis*, *M. tenuis*). *Sphenia* species tend to live attached to shells or stone, while *Cryptomya* species are found within the burrows of other invertebrates (Zhang et al. 2012, see also Coan 1999 for *Sphenia* characteristics). The name of the genus reflects individual's ability to be buried deep within the sediment despite short siphons (*kryptos* = hidden, *myax* = shellfish) as they utilize the burrows of other burrowers (Coan and Valentich-Scott 2012).

Description

Size: Individuals average 20 mm in length, but are found up to 30 mm (Haderlie and Abbott 1980; Lawry 1987). The illustrated specimen (from Coos Bay) is 21 mm in length (Fig. 1).

Color: Exterior chalky and white and yellowish, with dull reddish brown periostracum (Lawry 1987). Interior glossy white with spoon-shaped tooth on the right valve orange in color.

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Myoid bivalves are burrowers and borers, with long siphons and hinges with few teeth (Coan and Valentich-Scott 2007), although *C. californica* has relatively short siphons (Fig. 6). A distinctive feature of the Myidae is the presence of a strongly projecting chondrophore that is spoon or peg-shaped and is present on the left valve only (see Plate 395H, Coan and Valentich-Scott 2007).

Body: (see Fig. 319, Kozloff 1993).

Color:

Interior: Ligament is internal and seated in a shallow resilifer (a pit or groove). In right valve, the ligament is orange, leathery, and corresponds with the chondrophore on the left valve (Figs. 3, 4). Esophagus and stomach are surrounded by extensive intestinal diverticula, which extend from the right side of the stomach to the posterior portion of the foot, passing through the heart dorsally. The rectum is positioned dorsally and posterior to the adductor muscle. The anus is situated inside the excurrent siphon (Lawry 1987; Yonge 1951). A crystalline style (consisting of a gelatinous cortex and liquid core, Lawry 1987) resides in a sac lined with cilia, which allow it to rotate and press against the gastric shield of the stomach to aid in digestion (Lawry 1987). The crystalline style contains starch-hydrolyzing enzyme amylase and rotation rates range from 7 to 30 rpm (at 10–21°C). Within the crystalline style are mutualistic bacteria of the genus *Cristispira*. These spirochetes benefit from food particles concentrated by *C. californica* and the clam presumably benefits from an aid in digestion (Lawry et al. 1981; Lawry 1987). (For further information on digestion in *C. californica*, see Lawry 1987).

Exterior:

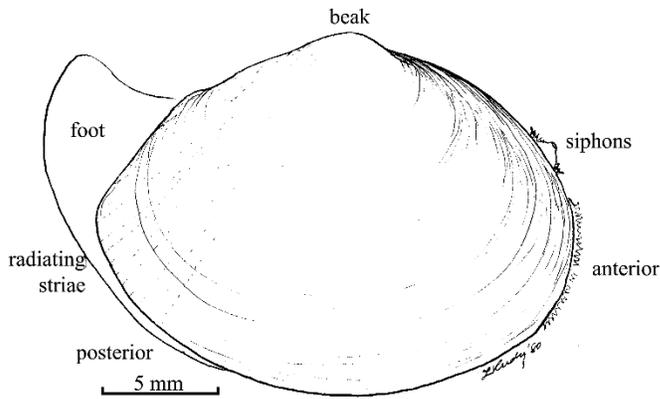
Byssus:

Gills: Gills pump water through the mantle cavity. They are large and covered in cilia that concentrate and transport food particles. Undigestible material is sorted by the labial palps and egested as pseudofeces, which are expelled through the incurrent siphon (Lawry 1987; Yonge 1951).

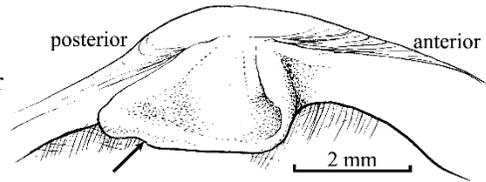
Shell: Shell is thin, fragile with external thin and brown periostracum and light concentric sculpture (Quayle 1970). The overall shape is oblong and gapes posteriorly (Haderlie and Abbott 1980).

Interior: Adductor muscle scars equal (family Myidae). Pallial line is entire and forms a right angle posteriorly (Fig. 3). The pallial sinus is absent (or inconspicuous) in members of the genus *Cryptomya* (Fig. 3). The chondrophore

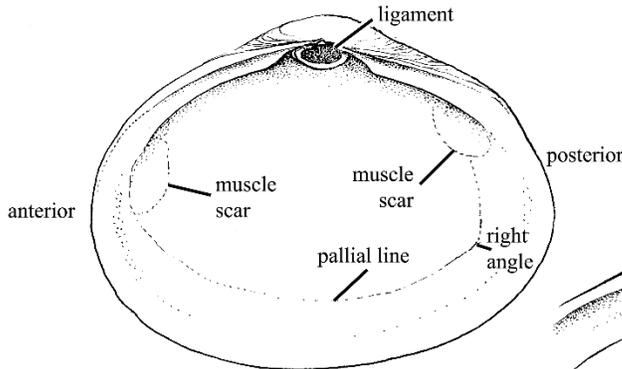
Cryptomya californica



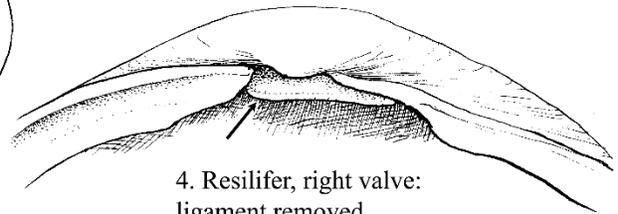
1. *Cryptomya californica*, exterior, right valve (L:2.1mm) x4.25: beaks central; anterior rounded, posterior truncate, gaping, concentric sculpture, same radial striae; shell thin, fragile, chalky white; siphons very short.



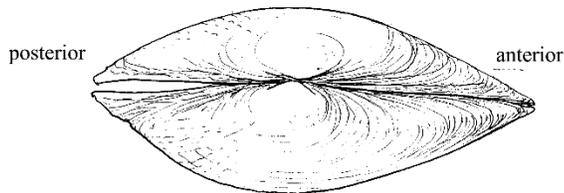
2. Chondrophore, left valve x11: spoon-shaped, broad, horizontal.



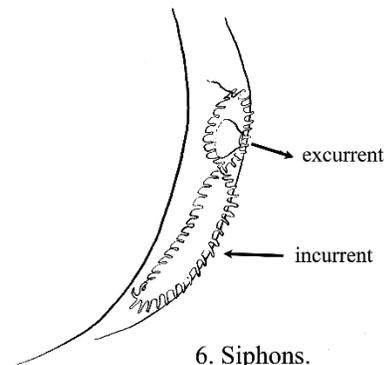
3. Interior, right valve: glossy white; anterior and posterior muscle scars equal; no cardinal or lateral hinge teeth; no pallial sinus, pallial line entire, forms a right angle posteriorly.



4. Resilifer, right valve: ligament removed.



5. (Dorsal view): posterior gapes slightly; no external ligament.



6. Siphons.

is broad, horizontal, and projecting (left valve only). The right valve is with resilifer to receive the chondrophore.

Exterior: The right valve is more convex than the left (McLean 1969). The shell sculpturing is similar to *M. arenaria*, but smaller (Haderlie and Abbott 1980). The beak is central and fairly prominent (Fig. 1).

Hinge: No true teeth or hinge plate, except for chondrophore and resilifer (Myidae, McLean 1969).

Eyes:

Foot: Foot extends through pedal gape and facilitates digging (Fig. 1). Individuals dig with muscular contractions of the foot coupled (making the foot appear alternatively knife and spade-shaped) with its epidermal ciliary action. Individuals are anchored by the foot and pull themselves onto the anteroventral portion of the shell. They then rock back and forth in a dorsoventral plane, working themselves into the substrate to completely bury themselves (except the siphons) in 5 minutes (Lawry 1987).

Siphons: Siphons are short (less than 1 mm in length), oval, and white (Coan and Valentich-Scott 2007). The excurrent siphon opening is controlled by a membrane, and both siphons possess an outer tentacular ring (Lawry 1987). The incurrent siphon is surrounded by additional tentacles and the excurrent siphon is short and vase-like (Fig. 6).

Burrow: Individuals found in burrows up to 50 cm deep (Haderlie and Abbott 1980; Lawry 1987). For digging behavior see **Foot**. Inhabits the burrows of other invertebrates (e.g., *Callianassa californiensis*, *Upogebia pugettensis*, *Urechis caupo*) and extends short siphons into burrow. *Cryptomya californiensis* receives oxygen, food, and can remove waste by utilizing these burrows (Lawry 1987).

Possible Misidentifications

There are five bivalve subclasses based on morphology and fossil evidence and one of those is the diverse Heterodonta. Recent molecular evidence (18S and 28S rRNA) suggests that the heterodont order Myoida is non monophyletic (Taylor et al. 2007). The family Myidae includes 25–40 species worldwide, which can be divided into groups such as those that are burrowing (*Mya*), those that are attached to shells or stone (*Sphenia*)

or those utilizing the burrows of other species (*Cryptomya*, *Paramya*) (Zhang et al. 2012). Characters of the Myidae include a shell that is not cemented to the substratum, valves that are (relatively) morphologically similar, a dorsal margin without ears, a hinge with an internal ligament in a distinct resilifer or chondrophore that is spoon shaped and present on the left valve (Coan and Valentich-Scott 2007). *Cryptomya* species are characterized by hinge without tooth-like process anteriorly on the right valve. *Mya*, on the other hand, have thick shells, gaping anteriorly and posteriorly and commarginal growth lines (Zhang et al. 2012).

There are only three local myid species including *Platyodon cancellatus*, *Mya arenaria* (see description in this guide) and *Cryptomya californica*. *Platyodon cancellatus* can be distinguished from the latter two species because its shells are heavy and with wavy commarginal sculpture and a round anterior. It has a truncate, gaping posterior end covered with periostracum. It also bores into rock and hard clay while *M. arenaria* and *C. californica* burrow into sand or mud. The shells of the two latter species are relatively thin. In *M. arenaria*, the pallial sinus is deep and individuals reach sizes of 120 mm, while in *C. californica* the pallial sinus is shallow, inconspicuous and individuals tend to be smaller (30 mm) (Coan and Valentich-Scott 2007). *Mya arenaria* is found as deep as 30 cm and is not necessarily near *Callianassa* burrows, where one might find *C. californica*. The siphons are *M. arenaria* are also longer than those of *C. californica* (Figs. 1, 6). Additionally, *Sphenia luticola* is a myid species that may occur in our area, but is found offshore in rocks and within kelp holdfasts (Coan and Valentich-Scott 2007). Juvenile *Mya* are not easily distinguished from *Sphenia* species, but *Mya* can be recognized by a large continuous pallial sinus (Coan 1999).

Cryptomya californica can be distinguished from other small white clams (*Macoma* spp., for instance) by its lack of any external ligament, the fragility of its shell, and internally, by its lack of hinge teeth, and presence of the chondrophore in the left valve. The Mactridae, including the gaper clam, have a chondrophore in both valves. However, mactrid adults are large, gape widely, and have small hinge teeth (which

Myidae lack). Their posterior edges are also truncate, not rounded, and their siphons are leather-like at the tips.

Ecological Information

Range: Type locality is Santa Barbara, California (Keen 1966). Gulf of Alaska to northern Peru (Chicagot Island) (Keen 1971; Haderlie and Abbott 1980).

Local Distribution: In bays and estuarine mudflats and sand flats where *Callianassa* or *Upogebia* beds are found. In Coos Bay, sites include the airport extension site, Pigeon Point, and South Slough, among others. Other Oregon estuaries where *C. californica* occurs include Tillamook, Netarts, Nestucca (Hancock et al. 1979), Yaquina, and also offshore (Lawry 1987).

Habitat: Sand and sandy mud, nearly always with siphons extending into the burrow of *Callianassa californiensis*, the ghost shrimp (which, in turn, often inhabits oyster beds). Individuals also occurs in muddy gravel and rocks on the open coast (Haderlie and Abbott 1980; Coan and Valentich-Scott 2007).

Salinity: Collected at salinities of 30.

Temperature: Occurs over a wide range of water temperatures geographically (see **Range**).

Tidal Level: Individuals can be found to 6 meters below the surface (Quayle 1970) as well as the upper to mid-intertidal zones. Individuals also found in the low intertidal and subtidal on the open coast (Haderlie and Abbott 1980) and are common in lower estuarine mudflats, up to +0.3 meters (Lawry 1987).

Associates: The burrows of *Callianassa californiensis* can include a community of marine invertebrates including the polynoid polychaete *Hesperonoe complanata*, three different pinnotherid (pea) crabs (e.g., *Fabia concharum*, Haderlie and Abbott 1980), and the goby, *Clevelandia ios*. This *Callianassa-Cryptomya* complex of organisms often co-occurs with *Sanguinolaria nuttallii* (Peterson 1984). *Cristispira* populations are constantly replenished by ingestion of bacteria from the environment (populations decrease when individuals are maintained in the laboratory with filtered seawater, Lawry 1987).

Cryptomya californica individuals also have a commensal association with the mud shrimp, *Upogebia pugettensis*, and the spoon worm, *Urechis caupo* (McLean 1969; Lawry 1987;

Coan and Valentich-Scott 2007). An average of eight *C. californica* were observed per *U. pugettensis* burrow (Griffin et al. 2004). Finally, amebocytes, spirochetes (*Cristispira*), and gram negative bacteria (*Vibro* spp.) are often observed near or concentrated within the crystalline style and stomach (Lawry 1987).

Abundance: Individuals can be very common and, in some parts of Coos Bay, it is the most abundant bivalve (e.g., airport mudflat, North Bend) (Gonor et al. 1979). This common estuarine species is, thus, often used in toxicity and biomarker tests (e.g., DDT, Ferraro and Cole 1997).

Life-History Information

Reproduction: Sperm acrosome is 5 μm in length and is tapered and slightly curved; the total sperm length (including flagellum) is 45 μm . Oocytes are oblong and 65 μm x 53 μm , with nucleus that is 30 μm , and nucleolus that is 13 μm (see Fig. 4c, d, Lawry 1987). The development of *C. californica* has not been described (Brink 2001).

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the "D" shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone. Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig. 1, Kabat and O'Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001.)

Juvenile:

Longevity:

Growth Rate:

Food: Filters material from water pumped into the burrows of commensal species.

Upogebia pugettensis and *Urechis caupo* are

more effective detritus filterers than *Callianassa californiensis*, and *Cryptomya californica* ingests more in the burrow of the latter species (MacGinitie and MacGinitie 1949). Individuals compete for suspended particles with extra large gills providing a larger surface area for filtering (Haderlie and Abbott 1980; Kozloff 1993). Ingested items include detritus, diatoms, bacteria, dinoflagellates, crustaceans and annelids. The *Upogebia-Cryptomya* complex is capable of filtering 100% of carbon from overlying water in one day (4.66×10^5 to 1.86×10^6 g Cd⁻¹, Griffen et al. 2004). The portion of suspended material removed by *C. californica* increases with increasing phytoplankton concentrations (Griffen et al. 2004).

Predators: Individuals remain relatively protected within their burrow. The invasive green crab, *Carcinus maenas*, has been known to eat *C. californica* (Palacios and Ferraro 2003)

Behavior: Interestingly, individuals remain just below the surface as a short-siphoned clam of its size normally would, however, they can live deep within the substrate, by utilizing the burrows of other species (see **Foot**, **Associates**, and **Burrow**).

Bibliography

- BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
- COAN, E. V. 1999. The eastern Pacific species of *Sphenia* (Bivalvia: Myidae). *Nautilus*. 113:103-120.
- COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
- . 2012. Bivalve seashells of tropical West America: marine bivalve mollusks from Baja California to northern Peru. Part 1. Santa Barbara Museum of Natural History, Santa Barbara.
- FERRARO, S. P., and F. A. COLE. 1997. Effects of DDT sediment-contamination on macrofaunal community structure and composition in San Francisco Bay. *Marine Biology*. 130:323-334.
- GONOR, J. J., D. R. STREHLOW, and G. E. JOHNSON. 1979. Ecological assessments at the North Bend airport extension site. School of Oceanography, Oregon State University, Salem, OR.
- GRIFFEN, B. D., T. H. DEWITT, and C. LANGDON. 2004. Particle removal rates by the mud shrimp *Upogebia pugettensis*, its burrow, and a commensal clam: effects on estuarine phytoplankton abundance. *Marine Ecology Progress Series*. 269:223-236.
- HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In*: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
- HANCOCK, D. R., T. F. GAUMER, G. B. WILLEKE, G. P. ROBERT, and J. FLYNN. 1979. Subtidal clam populations: distribution, abundance, and ecology. Oregon State University, Sea Grant College Program, Corvallis.
- KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In*: Reproduction and development of marine invertebrates of the northern Pacific Coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
- KEEN, A. M. 1966. West American mollusk types at the British Museum (Natural History). 1. T. A. Conrad and the Nuttall Collection. *Veliger*. 8:167-172.
- . 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. Stanford University Press, Stanford, CA.
- KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
- LAWRY, E. V. 1987. *Cryptomya californica* (Conrad, 1837): observations on its habitat, behavior,

- anatomy, and physiology. *Veliger*. 30:46-54.
15. LAWRY, E. V., H. M. HOWARD, J. A. BAROSS, and R. Y. MORITA. 1981. The fine-structure of cristispira from the lamellibranch *Cryptomya californica* (Conrad). *Current Microbiology*. 6:355-360.
 16. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 17. MCLEAN, J. H. 1969. Marine shells of southern California. Los Angeles County Museum of Natural History and Science, Los Angeles.
 18. PALACIOS, K. C., and S. P. FERRARO. 2003. Green crab (*Carcinus maenas* Linnaeus) consumption rates on and prey preferences among four bivalve prey species. *Journal of Shellfish Research*. 22:865-871.
 19. PETERSON, C. H. 1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points. *American Naturalist*. 124:127-133.
 20. QUAYLE, D. B. 1970. The intertidal bivalves of British Columbia. British Columbia Provincial Museum, Victoria, BC, Canada.
 21. TAYLOR, J. D., S. T. WILLIAMS, E. A. GLOVER, and P. DYAL. 2007. A molecular phylogeny of heterodont bivalves (Mollusca: Bivalvia: Heterodonta): new analyses of 18S and 28S rRNA genes. *Zoologica Scripta*. 36:587-606.
 22. YONGE, C. M. 1951. Studies on Pacific Coast mollusks. I. On the structure and adaptations of *Cryptomya californica* (Conrad). University of California (Berkeley) Publications in Zoology. 55:395-400.
 23. ZHANG, J., F. XU, and R. LIU. 2012. The Myidae (Mollusca, Bivalvia) from Chinese waters with description of a new species. *Zootaxa*:39-60.

Updated 2015

Mya arenaria

Soft-shelled clam

Phylum: Mollusca
Class: Bivalvia; Heterodonta
Order: Myoida
Family: Myidae

Taxonomy: *Mya arenaria* is this species original name and is almost exclusively used currently. However, the taxonomic history of this species includes many synonyms, overlapping descriptions, and/or subspecies (e.g. *Mya hemphilli*, *Mya arenomya arenaria*, Winckworth 1930; Bernard 1979). The subgenera of *Mya* (*Mya mya*, *Mya arenomya*) were based on the presence or absence of a subumbonal groove on the left valve and the morphology of the pallial sinus and pallial line (see Bernard 1979).

Description

Size: Individuals range in size from 2–150 mm (Jacobson et al. 1975; Haderlie and Abbott 1980; Kozloff 1993; Maximovich and Guerassimova 2003) and are, on average, 50–100 mm (Fig. 1). Mean weight and length were 74 grams and 8 cm (respectively) in Wexford, Ireland (Cross et al. 2012).

Individual weight varies seasonally and is greatest just before spawning and the smallest just after (range, 100–200 mg ash-free dry weight, Wadden Sea, Zwartz 1991).

Color: White with gray or dark, yellowish brown periostracum on shell edges, creating a rough outermost layer. Siphons are dark (Haderlie and Abbott 1980; Kozloff 1993; see Fig. 3, Zhang et al. 2012)

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Myoid bivalves are burrowers and borers, with long siphons and hinges with few teeth (Coan and Valentich-Scott 2007).

Body: Body is egg-shaped in outline (Fig. 1; Ricketts and Calvin 1952) (see Fig. 305, Kozloff 1993).

Color:

Interior: A crystalline style (consisting of a gelatinous cortex and liquid core, Lawry 1987) resides in a sac lined with cilia. The cilia allow the style to rotate and press against a gastric shield within the stomach, aiding in

digestion (Lawry 1987). In *M. arenaria*, the crystalline style can be regenerated after 74 days (Haderlie and Abbott 1980) and may contribute to the clam's ability to live without oxygen for extended periods of time (Ricketts and Calvin 1952). The ligament is white, strong, and entirely internal (Kozloff 1993). Two types of gland cells (bacillary and goblet) comprise the pedal aperture gland or glandular cushion located within the pedal gape. It is situated adjacent to each of the two mantle margins and aids in the formation of pseudofeces from burrow sediments; the structure of these glands may be of phylogenetic relevance (Norenburg and Ferraris 1992).

Exterior:

Byssus:

Gills:

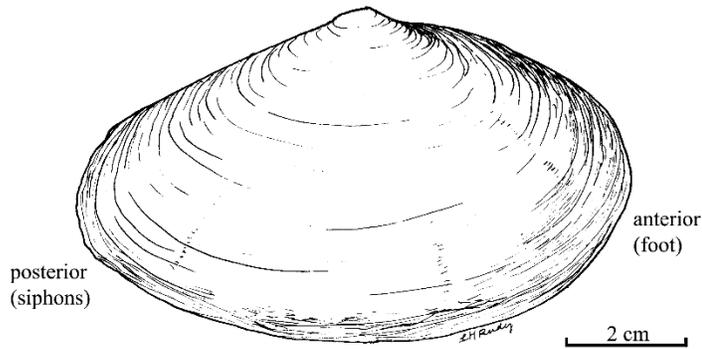
Shell: Shell is soft, thin, fragile (hence “soft shell clam”, Kozloff 1993; Coan and Valentich-Scott 2007), and composed completely of aragonite (MacDonald and Thomas 1980). The valves have an oval and rounded anterior and a pointed posterior (Kozloff 1993) and gape at each end (Haderlie and Abbott 1980). External shell sculpture is with concentric rings (Fig. 1).

Interior: Deep pallial sinus and spoon-shaped chondrophore, or triangular projection, is present on the left valve only (Haderlie and Abbott 1980; Kozloff 1993). Left and right adductor muscle scars are the same size but very different in shape (Fig. 2).

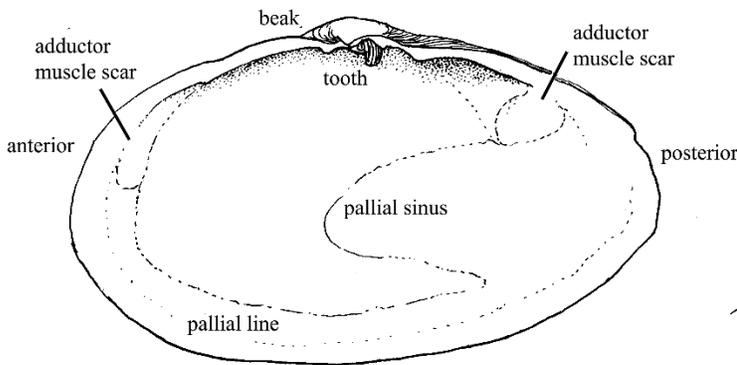
Exterior: Left and right valves are of similar morphology, which is long and egg-shaped, with shells convex, thin and brittle (Fig. 4). Low concentric growth striae on anterior and posterior ends are different: anterior are more blunt and posterior are pointed, but both ends gaping (Packard 1918). Beaks small, bent posteriorly, and slightly anterior of center (Fig. 2).

Hinge: Valve areas dissimilar and with spoon-shaped chondrophore in left valve. Right valve is with tooth in opposition to chondrophore (Fig. 3). No hinge plate teeth (cardinal or lateral).

Mya arenaria

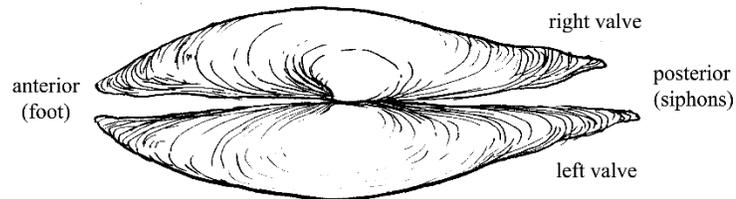
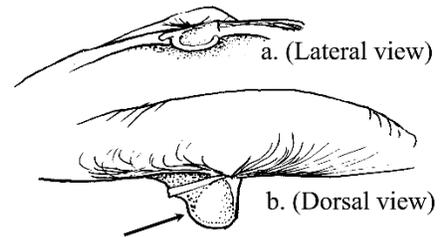


1. *Mya arenaria*, exterior, right valve x1:
shell egg-shaped, thin, brittle; concentric growth rings, small beaks; both ends rounded, slightly gapping.



2. Interior, right valve:
white; muscle scars alike; pallial sinus deep, no cardinal teeth; ligament completely internal; tooth opposing chondrophore.

3. Hinge area, left valve:
chondrophore spoon-shaped.



4. (Dorsal view)

Eyes:**Foot:**

Siphons: Long, large siphons are fused, non-retractable (Coan and Valentich-Scott 2007; Tan and Beal 2015), and dark in color (Haderlie and Abbott 1980).

Burrow: Unlike the other local member of the Myidae, *Cryptomya californica* (see description in this guide), *M. arenaria* has long siphons and can be found in relatively deep burrows up to 40 cm (Haderlie and Abbott 1980; Kozloff 1993; Coan and Valentich-Scott 2007; González et al. 2015).

Possible Misidentifications

There are five bivalve subclasses based on morphology and fossil evidence and one of those is the diverse Heterodonta. Recent molecular evidence (18S and 28S rRNA) suggests that the heterodont order Myoida is non monophyletic (Taylor et al. 2007). The family Myidae includes 25–40 species worldwide, which can be divided into groups such as those that are burrowing (*Mya*), those that are attached to shells or stone (*Sphenia*) or those utilizing the burrows of other species (*Cryptomya*, *Paramya*) (Zhang et al. 2012). Characters of the Myidae include a shell that is not cemented to the substratum, valves that are (relatively) morphologically similar, a dorsal margin without ears, a hinge with an internal ligament in a distinct resilifer or chondrophore that is spoon shaped and present on the left valve (Coan and Valentich-Scott 2007). *Cryptomya* species are characterized by hinge without tooth-like process anteriorly on the right valve. *Mya*, on the other hand, have thin shells, gaping anteriorly and posteriorly and commarginal growth lines (Zhang et al. 2012).

There are only three local myid species including *Platyodon cancellatus*, *Mya arenaria* and *Cryptomya californica* (“the false *Mya*” see description in this guide). *Platyodon cancellatus* can be distinguished from the latter two species because its shells are heavy and with wavy commarginal sculpture and a round anterior. It has a truncate, gaping posterior end covered with periostracum. It also bores into rock and hard clay while *M. arenaria* and *C. californica* burrow into sand or mud. The shells of the two latter species are relatively thin. In *M. arenaria*, the pallial sinus is deep and individuals reach sizes of 150 mm, while in *C.*

californica the pallial sinus is shallow, inconspicuous and individuals tend to be smaller (30 mm) (Coan and Valentich-Scott 2007). *Mya arenaria* is found as deep as 40 cm and is not necessarily near *Callianassa californiensis* burrows, where one might find *Cryptomya californica*. The siphons are *M. arenaria* are also longer than those of *C. californica* (see *C. californica*, Figs. 1, 6 in this guide). Additionally, *Sphenia luticola* is a myid species that may occur in our area, but is found offshore in rocks and within kelp holdfasts (Coan and Valentich-Scott 2007). Juvenile *Mya* are not easily distinguished from *Sphenia* species, but *Mya* can be recognized by a large continuous pallial sinus (Coan 1999).

Mya arenaria may be confused with other local common clams, e.g. *Saxidomus*, *Tresus*, *Tellina* or *Macoma* species. These genera do not have an internal ligament or a chondrophore. Small *Tresus* can otherwise be mistaken for *M. arenaria*. Small Tellinid clams have an external ligament without a nymph, and lateral hinge teeth, which *M. arenaria* lack. *Macoma* species (see descriptions in this guide) are very like *Tellina*, but their shells are always a bit flexed, they have no lateral teeth, and no internal coloration. Furthermore, where *M. arenaria* is abundant is in upper reaches of estuaries where salinity is reduced, species in the genera *Saxidomus* and *Tresus* are not usually found.

Ecological Information

Range: Type locality is Europe (Zhang et al. 2012). Current eastern Pacific distribution from Alaska to San Diego, California (Haderlie and Abbott 1980). Current populations introduced from the Atlantic coast with oyster spat in 1874 in San Francisco (Coan and Valentich-Scott 2007), although it appears in the fossil record (Ricketts and Calvin 1971) in California and Vancouver (Packard 1918). However, *M. arenaria* is not represented in local Native American mounds (Kozloff 1993). The palaeontological history of *M. arenaria* was described by Fujie (1957, 1962), as the species originated in the Pacific in the Miocene, spread to the Atlantic into the Pliocene, became extinct in the Pacific northwest by the Pleistocene was re-established and introduced from Atlantic populations in 1880s and was re-introduced

to the eastern Atlantic and Pacific during the Pleistocene (Rasmussen and Heard 1995; Zhang et al. 2012). Following introduction, *M. arenaria* spread northward to Willapa Bay, Washington in 1880 and Alaska in 1950s (Haderlie and Abbott 1980; Ricketts and Calvin 1952). Common on the Atlantic Coast and Europe in areas of low salinity (e.g. Baltic Sea, Kozloff 1993). It has crowded out the native *Macoma* spp. on the Pacific coast in some areas (Keep and Longstreth 1935). In the Cold Temperate Northwest Atlantic biogeographic province, six genetic clusters of *M. arenaria* were observed spanning seven distinct ecoregions. Those to the north were defined by geographic barriers and selection processes and those to the south were likely the result of and increased with geographic distance only (St-Onge et al. 2013).

Local Distribution: Local distribution in Coos and Yaquina Bay as well as the Suislaw, Umpqua, Tillamook, Alsea and Columbia estuaries.

Habitat: Mud and sand of bays with sand, mud, gravel mix (Kozloff 1993; Coan and Valentich-Scott 2007), often in upper reaches where salinity is reduced, but requires complete protection, as it cannot burrow or maintain itself in a shifting substratum (Ricketts and Calvin 1971). Very tolerant of extreme conditions (e.g., anaerobic or foul mud, brackish water, temperatures below freezing, Ricketts and Calvin 1971; Haderlie and Abbott 1980). Can live without oxygen for eight days (Ricketts and Calvin 1952) and it is thought that the shell serves as an alkaline reserve to neutralize lactic acid from anaerobic respiration (Haderlie and Abbott 1980). In a study testing the effects ocean acidification on *M. arenaria*, sedimentary aragonite saturation resulted in a negative relationship with dispersal and a positive relationship with clam burrowing depth (Clements and Hunt 2014). Conversely, increases in proton concentration yielded a negative relationship with burrowing depth (Clements and Hunt 2014). Thermal stress (e.g., associated with climate change) is accompanied by oxidative stress in marine mollusks, including *M. arenaria*, and leads to the mitochondrial production of reactive oxygen species (Abele et al. 2002). *Mya arenaria* individuals respond to hypoxia by reducing burrow depth and increasing siphon extension (Taylor and Eggleston 2000).

Salinity: Tolerates brackish water and reduced salinity, as well as full salt water (Haderlie and Abbott 1980; Kozloff 1993).

Temperature: Range limited to cool areas, although this species can also tolerate temperatures below freezing (Ricketts and Calvin 1952). Eastern Atlantic southern distribution set by critical maximum temperature of 28°C (Rasmussen and Heard 1995).

Tidal Level: Found from 15–40 cm depths in mud habitats (Packard 1918) and intertidal to 20 m (Zhang et al. 2012).

Associates: Commensal pea crabs, *Fabia subquadrata*, *F. concharum*, *Pinnixa faba*, *P. littoralis* (Ricketts and Calvin 1971; Haderlie and Abbott 1980). Co-occurs with *Macoma balthica* and the lugworm, *Arenicola marina*, in the Wadden Sea (Günther 1992; Strasser et al. 1999). The abundance of *A. marina*, a bioturbator, has a negative effect on recruitment in *M. arenaria* (Strasser et al. 1999). Domoic acid (a neurotoxin), released from and ingested with the diatom *Pseudo-nitzschia*, is biodegraded in *M. arenaria* with the help of autochthonous bacteria (Stewart et al. 1998).

Abundance: *Mya arenaria* can be very abundant and often occurs with a patchy distribution (e.g., 177 individuals/m², St. Lawrence estuary, Roseberry et al. 1992). Locally abundant in Yaquina, Siuslaw, and Umpqua estuaries, and in some parts of Coos Bay where it is “fairly common” (Haderlie and Abbott 1980). *Mya arenaria* was reported as ubiquitous in northeast and northwest Atlantic (Tan and Beal 2015). In the Wadden Sea, 50 individuals/m² were observed (Strasser et al. 1999; Günther 1992), and up to 1,000 individuals/m² reported in Kandalaksha Bay, White Sea (Maximovich and Guerassimova 2003). This common estuarine species is often used in toxicity and biomarker tests, where effects of tributyltin (TBT) included masculinizing of females, sex ratios skewed toward male, and delayed male maturation (Gagné et al. 2003).

Life-History Information

Reproduction: Dioecious with, at most, two periods of sexual maturation and spawning, one in the fall (primary maturation period) and one in spring (secondary maturation) (Chesapeake Bay and St. Lawrence estuary, Roseberry et al. 1992). A continuous

reproductive period from April to October occurs in New England (Pfitzenmeyer and Shuster 1960). Atlantic species tend to spawn from June to August and eggs 60–80 μm diameter (Haderlie and Abbott 1980). In Cape Cod, gametogenesis began during late winter and spawning was complete by the end of summer (September, Ropes and Stickney 1965). Populations in Wexford, Ireland had sex ratios of 1:1.15 (female to male) and were ripe and spawning in August, completed in November (Cross et al. 2012). Life-history characteristics appeared to correlate along a latitudinal gradient in the northeast coast of the United States: individuals in southern populations grew faster, exhibited greater variation in juvenile mortality, had larger egg sizes (range 25–45 μm), lower egg density (range 495–1,541), decreased longevity (4–15 years), and larger size at maturation (see Table 1, Appeldoorn 1995). In San Francisco, CA, gametogenesis began in late February and spawning occurred from April to October (Rosenblum and Niesen 1985). Sperm morphology and spermatogenesis of the subspecies *Mya arenaria oonogai* was described by Kim et al. in 2011. In this species, the spermatozoon was approximately 50 μm in length. Disseminated neoplasia, a leukemia-like disease, occurs in the gonadal tissues of *M. arenaria* (Barber 1996; Boettger and Barletta 2015). The frequency of neoplasia increases in spring in Maine (Boettger and Barletta 2015). In 1994 in Whiting Bay, Maine, progressive and potentially lethal gonadal neoplasms were observed in 19% of individuals, involving up to 100% of gonadal follicles. Females were more likely to have neoplasms than males and produced fewer, smaller gametes leading to an overall negative impact on reproductive output (Barber 1996).

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the

“D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone. Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig. 1, Kabat and O’Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001.). Young *M. arenaria* larvae (150 μm) have a broadly rounded umbo with a short, sloping posterior (see Fig. 4, Brink 2001). The umbo becomes angled in advanced individuals and the shoulders become straight and steeply sloping. Eventually, the anterior and posterior ends elongate and are pointed and metamorphosis occurs when larvae are 170–230 μm (Chanley and Andrews 1971; Brink 2001). Settlement in the Wadden Sea occurs from May to June (Günther 1992) and in Mill Cove, New Brunswick, when individuals are greater than 500 μm (Morse and Hunt 2013). Settlement may depend on sediment properties (e.g., grain size, presence of sea grasses, Strasser et al. 1999). Juveniles and smaller individuals (< 2 mm) can also be transported hydrodynamically (Hunt and Mullineaux 2002). Maximum transport rates coincided (positive correlation) with peaks in bedload transport: in sheltered sandflats, maximum transport rate was 790 individuals/m/day and in exposed habitats, maximum transport rate increased to 2,600 individuals/m/day (Emerson and Grant 1991). Recruitment is highly variable and based on (among others) predation, temperature, and adult-larval interactions. Some research shows that larvae avoid settlement in areas with high conspecific density (Maximovich and Guerassimova 2003, but see Brousseau and Bagilvo 1988; Günther 1992).

Juvenile: Juveniles are typically less than 2–15 mm in length (Strasser et al. 1999; Tan and Beal 2015) and size is generally fixed by epibenthic predators. Sexual maturity occurs when individuals are 25–35 mm in length (Brousseau 1979; Rosenblum and Niesen 1985). Following settlement, significant changes occur in population distributions within the first month, due to post-settlement dispersal and predation (Morse and Hunt 2013). Newly settled individuals and juveniles are prey to a variety of epibenthic predators

and their size and abundance is ultimately controlled by predation (Hunt and Mullineaux 2002). Mortality by predation significantly decreases with growth. For example, green crabs (*Carcinus maenas*) reduced 80% of small (<17 mm) *M. arenaria* in caged experiments containing 1–5 crabs in Pomquet Harbour, Nova Scotia (Floyd and Williams 2004). Young *M. arenaria* (< 30 mm) were most susceptible to predation by the snail, *Lanutia heros*, as 3.5% died/year in the first five years (Maine, Commito 1982).

Ultimately, size selective feeding leads to overestimated average size measurements among juveniles and fast juvenile growth allows for a size refuge from epibenthic predators (Wadden Sea, Günther 1992). Additionally, juveniles escape predation with severe winters that result in mortality of predators (Günther 1992). Mortality significantly decreased 94 days after settlement (Günther 1992).

Longevity: Up to 28 years (Appeldoorn 1995). A 17 years maximum was reported in Kandalasksha Bay, White Sea (Maximovich and Guerassimova 2003). Over 25 years of monitoring in the White Sea, populations of *M. arenaria* showed alternatively high and low levels of mortality (Table 2, Gerasimova et al. 2015). The authors attributed this variation in mortality to the unstable habitat early in life and intraspecific relationships and competition associated with dense aggregations (Gerasimova et al. 2015).

Growth Rate: Clams as small as 25 mm have been found to have mature gametes (Pfitzenmeyer and Shuster 1965). Individuals approximately 15 mm in length grew 110 μm per day (Günther 1992). Most shell deposition occurred from March to November in Gloucester, MA (Brousseau 1979). Although external growth rings can be conspicuous, they may not be an accurate indicator of clam age and are not always clearly defined. Instead, internal growth lines, which can be seen in thin sections when shells are sliced from the umbo to the ventral margin, reliably indicate growth in late spring months before spawning (Prince Edward Island, MacDonald and Thomas 1980). The neoplastic disease, disseminated neoplasia, which is characterized by excessive and abnormal cell growth is found in *M. arenaria* and appears to be transmitted among

populations by horizontal transmission (Carballal et al. 2015).

Food: A suspension and filter feeder (Tan and Beal 2015), *M. arenaria* takes up oxygen, food, algae, and detritus containing iron (Fe) and other trace metals (González et al. 2015) by filtering seawater. Compared to other filter feeders, *M. arenaria* may have a low filtration rate (Jorgensen 1966 in Vincent et al. 1988). Individuals can adapt to varying algal concentrations; a low concentration leads to a reduced siphon opening and valve gape, which can occur after several hours of reduced concentrations, while an increase in algal concentration leads to siphon opening within 5–20 min (Riisgard et al. 2003).

Predators: Shorebirds (e.g., sea gulls), sea otters eat exposed adults and larvae are preyed upon by planktonic predators and suspension feeders. Adults are prey to infaunal predators (e.g., gastropods, nemertean) and juveniles live so close to the sediment surface that their siphons are often nipped off by crustaceans and fish (Tan and Beal 2015). Additional predators include fish, shrimp, sandworms, crabs (e.g., the green crab, *Carcinus maenas*, Wong 2013; Morse and Hunt 2013; Tan and Beal 2015, the blue crab (*C. sapidus*, Taylor and Eggleston 2000), snails (Cross et al. 2012), the stingray, *Dasyatis sabina* (Rasmussen and Heard 1995), and *Nereis virens* (Morse and Hunt 2013). Predation by *Polinices duplicatus*, increased with temperature, with individuals ingesting as many as 96 *Mya arenaria*/snail/year (Edwards and Huebner 1977). *Carcinus maenas* (green crab) populations decrease populations of *M. arenaria* and survival of clams was seven times greater when predation by green crabs was experimentally removed (Maine, Tan and Beal 2015). Also a commercially important species. In eastern Canada (e.g., Nova Scotia, New Brunswick) the fishery landed 4,500 tons in 1986 and 3,000 tons in 1988 (Aramaratunga and Misra 1989). Predators of newly settled larvae also include adults of the same species. There is a negative relationship between adult density and newly settled larvae in both *Cerastoderma edule* (40% mortality) and *M. arenaria* (20% mortality) (André and Rosenberg 1991). **Behavior:** In the presence of predators, individuals increase their burial depth and reduce growth (Tan and Beal 2015).

Preferred orientation is perpendicular to the principle component of current direction. This allows siphons to be in line with the current and, presumably, avoids inhalant exhalant contamination (Vincent et al. 1988).

Bibliography

1. ABELE, D., K. HEISE, H. O. PORTNER, and S. PUNTARULO. 2002. Temperature-dependence of mitochondrial function and production of reactive oxygen species in the intertidal mud clam *Mya arenaria*. *Journal of Experimental Biology*. 205:1831-1841.
2. AMARATUNGA, T., and R. K. MISRA. 1989. Identification of soft-shell clam (*Mya arenaria* Linnaeus, 1758) stocks in eastern Canada based on multivariate morphometric analysis. *Journal of Shellfish Research*. 8:391-398.
3. ANDRE, C., and R. ROSENBERG. 1991. Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria*. *Marine Ecology Progress Series*. 71:227-234.
4. APPELDOORN, R. S. 1995. Covariation in life-history parameters of soft-shell clams (*Mya arenaria*) along a latitudinal gradient. *ICES Marine Science Symposia*. 199:19-25.
5. BARBER, B. J. 1996. Effects of gonadal neoplasms on oogenesis in softshell clams, *Mya arenaria*. *Journal of Invertebrate Pathology*. 67:161-168.
6. BERNARD, F. R. 1979. Identification of living *Mya* (Bivalvia: Myoida). *Venus: the Japanese Journal of Malacology*. 38:185-204.
7. BOETTGER, S. A., and A. T. BARLETTA. 2015. Effect of reproductive effort on neoplasia development in the soft-shell clam, *Mya arenaria*. *Integrative and Comparative Biology*. 55:E17-E17.
8. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
9. BROUSSEAU, D. J. 1979. Analysis of growth rate in *Mya arenaria* using the Von Bertalanffy equation. *Marine Biology*. 51:221-227.
10. BROUSSEAU, D. J., and J. A. BAGLIVO. 1988. Life tables for two field populations of soft-shell clam, *Mya arenaria*, (Mollusca: Pelecypoda) from Long Island Sound. *Fishery Bulletin*. 86:567-579.
11. CARBALLAL, M. L., B. J. BARBER, D. IGLESIAS, and A. VILLALBA. 2015. Neoplastic diseases of marine bivalves. *Journal of Invertebrate Pathology*. 131:83-106.
12. CHANLEY, P. E., and J. D. ANDREWS. 1971. Aids for identification of bivalve larvae of Virginia. *Malacologia*. 11:45-119.
13. CLEMENTS, J. C., and H. L. HUNT. 2014. Influence of sediment acidification and water flow on sediment acceptance and dispersal of juvenile soft-shell clams (*Mya arenaria* L.). *Journal of Experimental Marine Biology and Ecology*. 453:62-69.
14. COAN, E. V. 1999. The eastern Pacific species of *Sphenia* (Bivalvia: Myidae). *Nautilus*. 113:103-120.
15. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
16. COMMITO, J. A. 1982. Effects of *Lunatia heros* predation on the population dynamics of *Mya arenaria* and *Macoma balthica* in Maine, USA. *Marine Biology*. 69:187-193.
17. CROSS, M. E., S. LYNCH, A. WHITAKER, R. M. O' RIORDAN, and S. C. CULLOTY. 2012. The reproductive biology of the softshell clam, *Mya arenaria*, in Ireland, and the possible impacts of climate variability. *Journal of Marine Biology*. 2012:1-9.
18. EDWARDS, D. C., and J. D. HUEBNER. 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. *Ecology*. 58:1218-1236.
19. EMERSON, C. W., and J. GRANT. 1991. The control of soft-shell clam

- (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. *Limnology and Oceanography*. 36:1288-1300.
20. FLOYD, T., and J. WILLIAMS. 2004. Impact of green crab (*Carcinus maenas* L.) predation on a population of soft-shell clams (*Mya arenaria* L.) in the Southern Gulf of St. Lawrence. *Journal of Shellfish Research*. 23:457-462.
 21. FUJIE, T. 1957. On the myarian pelecypods of Japan. Part I: Summary of the study of the genus *Mya* from Hokkaido. *Journal of the Faculty of Science Hokkaido University Geology*. 9:381-413.
 22. —. 1962. On the myarian pelecypods of Japan. Part II: Geological and geographical distribution of fossil and recent species, genus *Mya*. *Journal of the Faculty of Science Hokkaido University Geology*. 11:399-430.
 23. GAGNE, F., C. BLAISE, J. PELLERIN, E. PELLETIER, M. DOUVILLE, S. GAUTHIER-CLERC, and L. VIGLINO. 2003. Sex alteration in soft-shell clams (*Mya arenaria*) in an intertidal zone of the Saint Lawrence River (Quebec, Canada). *Comparative Biochemistry and Physiology: C-Toxicology & Pharmacology*. 134:189-198.
 24. GERASIMOVA, A. V., N. V. MAXIMOVICH, and N. A. FILIPPOVA. 2015. Cohort life tables for a population of the soft-shell clam, *Mya arenaria* L., in the White Sea. *Helgoland Marine Research*. 69:147-158.
 25. GONZALEZ, P. M., D. ABELE, and S. PUNTARULO. 2015. Oxidative status of respiratory tissues of the bivalve *Mya arenaria* after exposure to excess dissolved iron. *Marine and Freshwater Behaviour and Physiology*. 48:103-116.
 26. GUNTHER, C. P. 1992. Settlement and recruitment of *Mya arenaria* (L.) in the Wadden Sea. *Journal of Experimental Marine Biology and Ecology*. 159:203-215.
 27. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 28. HUNT, H. L., and L. S. MULLINEAUX. 2002. The roles of predation and postlarval transport in recruitment of the soft shell clam (*Mya arenaria*). *Limnology and Oceanography*. 47:151-164.
 29. JACOBSON, R. W., P. HEIKKILA, and K. S. HILDERBRAND. 1975. Oregon's captivating clams. Oregon State University Extension Service, Sea Grant Marine Advisory Program, and Oregon Dept. of Fish and Wildlife, Corvallis, Or.
 30. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 31. KEEP, J., and J. LONGSTRETH. 1935. West coast shells: a description in familiar terms of the principal marine, fresh-water, and land mollusks of the United States, British Columbia, and Alaska, found west of the Sierra. Stanford University Press, Stanford, CA.
 32. KIM, J., J. CHUNG, and Y. PARK. 2011. Ultrastructures of germ cells during spermatogenesis and taxonomic values in sperm morphology in male *Mya arenaria* oonogai (Heterodonta: Myidae). *Korean Journal of Malacology*. 27:377-386.
 33. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 34. LAWRY, E. V. 1987. *Cryptomya californica* (Conrad, 1837): observations on its habitat, behavior, anatomy, and physiology. *Veliger*. 30:46-54.
 35. MACDONALD, B. A., and M. L. H. THOMAS. 1980. Age determination of the soft-shell clam *Mya arenaria* using shell internal growth lines. *Marine Biology*. 58:105-109.

36. MAXIMOVICH, N. V., and A. V. GUERASSIMOVA. 2003. Life history characteristics of the clam *Mya arenaria* in the White Sea. *Helgoland Marine Research*. 57:91-99.
37. MORSE, B. L., and H. L. HUNT. 2013. Impact of settlement and early post-settlement events on the spatial distribution of juvenile *Mya arenaria* on an intertidal shore. *Journal of Experimental Marine Biology and Ecology*. 448:57-65.
38. NORENBURG, J. L., and J. D. FERRARIS. 1990. Cytomorphology of the pedal aperture glands of *Mya arenaria* L. (Mollusca, Bivalvia). *Canadian Journal of Zoology*. 68:1137-1144.
39. PACKARD, E. L. 1918. Molluscan fauna from San Francisco Bay. *Zoology*. 14:199-452.
40. PFITZENMEYER, H. T., and C. N. SHUSTER. 1960. A partial bibliography of the softshell clam *Mya arenaria* Linnaeus. Maryland Department of Research and Education, Chesapeake Biological Laboratories, Solomons, MD.
41. RASMUSSEN, E., and R. W. HEARD. 1995. Observations on extant populations of the softshell clam, *Mya arenaria* Linne, 1758 (Bivalvia: Myidae), from Georgia (USA) estuarine habitats. *Gulf Research Reports*. 9:85-96.
42. RICKETTS, E. F., and J. CALVIN. 1952. *Between Pacific tides*: an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford: Stanford University Press, Stanford.
43. —. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
44. RIISGARD, H. U., C. KITNER, and D. F. SEERUP. 2003. Regulation of opening state and filtration rate in filter-feeding bivalves (*Cardium edule*, *Mytilus edulis*, *Mya arenaria*) in response to low algal concentration. *Journal of Experimental Marine Biology and Ecology*. 284:105-127.
45. ROPES, J. W., and A. P. STICKNEY. 1965. Reproductive cycle of *Mya arenaria* in New England. *Biological Bulletin*. 128:315-327.
46. ROSEBERRY, L., B. VINCENT, and C. LEMAIRE. 1991. Growth and reproduction of *Mya arenaria* in their intertidal zone of the Saint Lawrence Estuary. *Canadian Journal of Zoology*. 69:724-732.
47. ROSENBLUM, S. E., and T. M. NIESEN. 1985. The spawning cycle of soft-shell clam, *Mya arenaria*, in San Francisco Bay. *Fishery Bulletin*. 83:403-412.
48. ST-ONGE, P., J. SEVIGNY, C. STRASSER, and R. TREMBLAY. 2013. Strong population differentiation of softshell clams (*Mya arenaria*) sampled across seven biogeographic marine ecoregions: possible selection and isolation by distance. *Marine Biology*. 160:1065-1081.
49. STEWART, J. E., L. J. MARKS, M. W. GILGAN, E. PFEIFFER, and B. M. ZWICKER. 1998. Microbial utilization of the neurotoxin domoic acid: blue mussels (*Mytilus edulis*) and soft shell clams (*Mya arenaria*) as sources of the microorganisms. *Canadian Journal of Microbiology*. 44:456-464.
50. STRASSER, M., M. WALENSKY, and K. REISE. 1999. Juvenile-adult distribution of the bivalve *Mya arenaria* on intertidal flats in the Wadden Sea: why are there so few year classes? *Helgoland Marine Research*. 53:45-55.
51. TAN, E. B. P., and B. F. BEAL. 2015. Interactions between the invasive European green crab, *Carcinus maenas* (L.), and juveniles of the soft-shell clam, *Mya arenaria* L., in eastern Maine, USA. *Journal of Experimental Marine Biology and Ecology*. 462:62-73.
52. TAYLOR, D. L., and D. B. EGGLESTON. 2000. Effects of hypoxia on an estuarine predator-prey interaction: foraging behavior and mutual interference in the blue crab *Callinectes sapidus* and the infaunal clam prey *Mya arenaria*. *Marine Ecology Progress Series*. 196:221-237.

53. TAYLOR, J. D., S. T. WILLIAMS, E. A. GLOVER, and P. DYAL. 2007. A molecular phylogeny of heterodont bivalves (Mollusca: Bivalvia: Heterodonta): new analyses of 18S and 28S rRNA genes. *Zoologica Scripta*. 36:587-606.
54. VINCENT, B., G. DESROSIERS, and Y. GRATTON. 1988. Orientation of the infaunal bivalve *Mya arenaria* (L.) in relation to local current direction on a tidal flat. *Journal of Experimental Marine Biology and Ecology*. 124:205-214.
55. WINCKWORTH, R. 1930. Notes on nomenclature. 5. Some new names for British marine bivalves. *Proceedings of the Malacological Society of London*. 19:14-15.
56. WONG, M. C. 2013. Green crab (*Carcinus maenas* Linnaeus, 1758) foraging on soft-shell clams (*Mya arenaria* Linnaeus, 1758) across seagrass complexity: Behavioural mechanisms and a new habitat complexity index. *Journal of Experimental Marine Biology and Ecology*. 446:139-150.
57. ZHANG, J., F. XU, and R. LIU. 2012. The Myidae (Mollusca, Bivalvia) from Chinese waters with description of a new species. *Zootaxa*:39-60.
58. ZWARTS, L. 1991. Seasonal variation in body weight of the bivalves *Macoma balthica*, *Scrobicularia plana*, *Mya arenaria* and *Cerastoderma edule* in the Dutch Wadden Sea. *Netherlands Journal of Sea Research*. 28:231-245.

Updated 2015

Penitella penita

A common piddock

Phylum: Mollusca
Class: Bivalvia, Heterodonta
Order: Myoida
Family: Pholadidae

Taxonomy: The taxonomies of both pholad species in this guide (*Z. pilsbryi* and *Penitella penita*) are extensive and complicated, including many synonyms and overlapping descriptions (for full list of synonymies see Kennedy 1974). *Penitella penita* was originally described as *Pholas penita* by Conrad in 1837. The current name was designated by Gabb in 1869 and the most common synonym seen today is *Pholadidea penita*. However, *Pholadidea* species differ from those in the genus *Penitella* by having a mesoplax that is divided longitudinally into two pieces, a feature not present in the latter genus (see *Penitella*, Kennedy 1974)

Description

Size: Individuals to 70–95 mm in length and 50 mm in height (Turner 1955; Haderlie and Abbott 1980; Kozloff 1993). The illustrated specimen (from Coos Bay) is 40 mm long, 18 mm high (Fig. 1).

Color: White, inside and out (Haderlie and Abbott 1980; Kozloff 1993).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Myoid bivalves are burrowers and borers, with long siphons and hinges with few teeth (Coan and Valentich-Scott 2007). Members of the Pholadidae bore into a variety of substrates, possess no pallets on siphon tips and have an anterior end that is pointed or curved with no notch (contrast to Teredinidae species, e.g. *Bankia setacea*, this guide) (see Plate 427F, 430D, Coan and Valentich-Scott 2007). While most pholad species are intertidal or subtidal, some can be found boring into wood at great depths (e.g. 7,250 meters *Xylophaga*, Kennedy 1974; Reft and Voight 2009; Voight 2009; Marshall and Spencer 2013).

Body:

Color: Foot and mantle white (Turner 1955).

Interior:

Exterior:

Byssus:

Ctenidia:

Shell: Shell shape is elongate, and divided into two distinct parts (Fig. 1). Shell anterior becomes worn away from burrowing abrasion (Evans and LeMessurier 1972), the addition of new shell creates a rough and bulbous anterior (Kozloff 1993). No periostracum is present.

Interior: Divided into three areas by pallial lines. The pallial sinus and posterior is with a large posterior muscle scar. The anterior muscle scar and accessory are unusually dorsal and a ventral muscle scar is also present (Fig. 4). An apophysis (myophore) is a short, narrow, spoon-shaped structure of each valve, which serves as an extra muscle attachment site for powerful grinding muscles (Keen 1971) (Fig. 4). In *P. penita* it is "weakly blade-like" (Turner 1955).

Exterior: The shell anterior is rounded, bulbous, and with rasp-like radial and concentric striae. These heavy file-like denticulations consist of a triangular rasping section which covers less than 1/2 valve area (Fig. 1, 3) (Kozloff 1993). The posterior is wedge-shaped, with regular concentric striations only, and a truncated end. Valves gape does not extend to the middle of the shell (*Penitella*, Keen and Coan 1974). A callum is present in adults (but not in young (Fig. 5)) at the anterior end (Fig. 1). Umbones are not prominent and umbonal reflection (where umbones turn posterior, Fig. 1) are closely appressed for the entire length (Coan and Valentich-Scott 2007). Siphonoplax is brown, membranous, heavy, flexible flaps, and is not lined with calcareous granules (Coan and Valentich-Scott 2007).

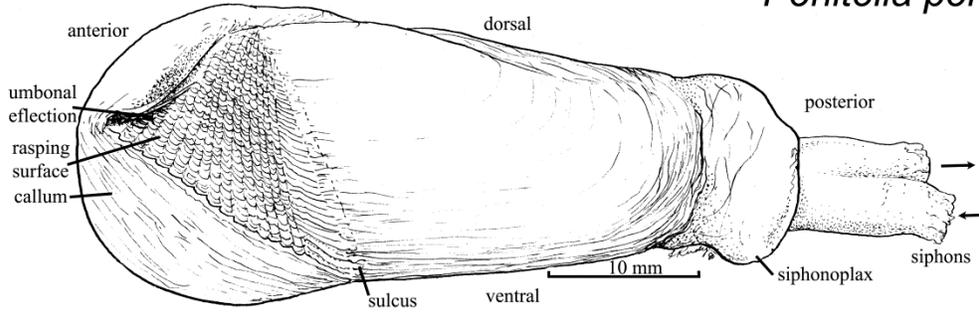
Hinge: No hinge teeth or ligament present.

Eyes:

Foot: Foot atrophies in adult individuals after the callum seals the shell anterior (Haderlie and Abbott 1980).

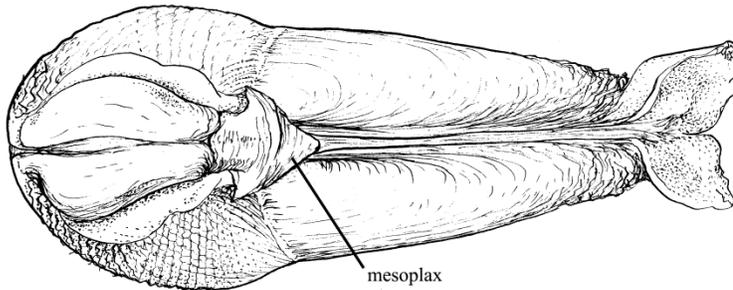
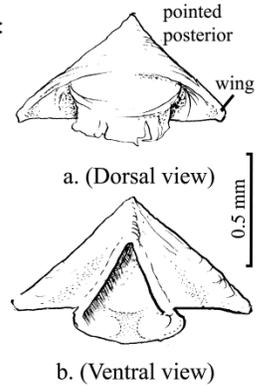
Siphons: Long, white, and retractible. The tips are marked with small red spots, but not

Penitella penita

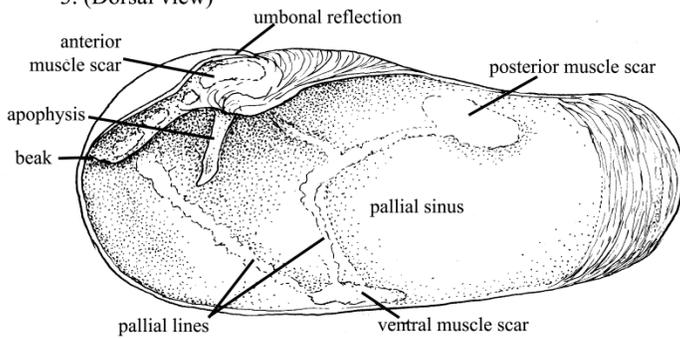


1. *Penitella penita* (L:40mm,W:18mm) x3: elongate shell divided into two distinct parts by umbonal-ventral sulcus; bulbous anterior with callum and rasping surface, posterior with concentric striae, truncate end; siphonoplax: heavy, brown flaps; siphons long, white, smooth.

2. Mesoplax x4.5

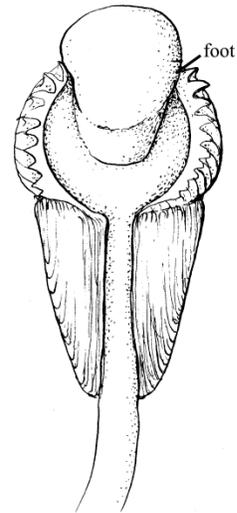


3. (Dorsal view)



4. Interior, right valve:

white; divided into three sections by two pallial lines; three muscle scars; apophysis: long, spoon-shaped.



5. Young (dorsal view) x3: no callum; foot exposed.

solidly red-tipped smooth. No warts or orange chitinous patches are present. No pallets are on siphon tips (compare to Teredinidae, e.g., *Bankia setacea*, this guide). Inhalant siphons with six large, and several small branched cirri around aperture (Turner 1955).

Burrow: (for burrow shape, see Fig 1B, Evans 1968d). Burrows are pear- (Haderlie 1981b) or cone-shaped (Evans and Fisher 1966; Evans 1968d). Burrows into stiff clay, sandstone, soft rock, shale and concrete (Haderlie and Abbott 1980; Kozloff 1993), up to 15 cm below the surface (at least 3 times the shell length). Burrowing mechanism is like that of the common local pholad, *Zirfaea pilsbryi* (see description in this guide): The foot is sucker-like and attaches to the substrate so that the shell can rotate slowly and create a cylindrical burrow. Shell valves rock back and forth by contractions of anterior and posterior adductor muscles. Individuals rotate after each stroke, making a cylindrical burrow (Lloyd 1896; Ricketts and Calvin 1952; Haderlie and Abbott 1980). Estimated burrowing rates varied with substrate type from 50 mm/year (soft substrates) to 50 mm/12 years (hard substrates, Evans 1968b), i.e., harder rock leads to a shallower burrow (Evans 1970). In Monterey, California, Haderlie (1981a) reported boring rates of 32 mm/year (2.6 mm/month). (see also **Habitat and Behavior.**)

Pholadidae-specific character

Mesoplax: A small accessory plate on dorsal edge (Fig. 2) has no accessory plates (e.g., protoplax, metaplax, hypoplax) present. The mesoplax is pointed posteriorly, and truncate anteriorly, with swept back lateral wing-like projections (Turner 1955).

Possible Misidentifications

There are several families of burrowing clams and the Pholadidae can be distinguished by their distinctively marked body areas (Fig. 1). Members of the Teredinidae and Pholadidae can be found locally. They can be distinguished by the absence of pallets on siphon tips in the latter family as well as an anterior end that is not notched, as in the Teredinidae. The Pholadidae includes 10 species locally, within the following genera: *Barnea* (*B. subtruncata*), *Chaceia* (*C. ovoidea*), *Netastoma* (*N. rostratum*), *Parapholas* (*P.*

californica), *Penitella* (five local species) and *Zirfaea* (*Z. pilsbryi*). The genus *Zirfaea* is characterized by adults that burrow into sand or mud, the absence of a callum in mature individuals, and a shell sculpture that is divided into two distinct zones (see Plates 427C, 429D, Coan and Valentich-Scott 2007). The genus *Barnea*, for example, also lacks a callum, but does not have these two distinct zones. All other local genera are characterized by the presence of a callum and all except *Netastoma* have a myophore as well. *Parapholas* species have shell sculpture with three distinct zones, where members of *Chaceia* and *Penitella* have two. None of the other local burrowing clams (e.g. in the genera *Hiatella*, *Entodesma*, *Barnea*, *Petricola*, *Bankia*) have distinct body areas or the bulbous, denticulated anterior of *Penitella*.

The genus closest to *Penitella*, and most likely to be confused with it, is *Zirfaea*. As mentioned above, *Penitella*'s valves are also divided into two distinct sections, but it differs in having a calcareous anterior callum, or accessory plate (in the adult) as well as a posterior which gapes only at the end, not to the middle of the shell (it has no anterior gape) and the apophysis is narrow, not broad. No *Penitella* species have a siphon longer than its body (Evans and Fisher 1966) and all *Penitella* species have retractable siphons. There are five species of *Penitella* in our area (see Coan and Valentich-Scott 2007).

Penitella conradi is very small and is found in *Mytilus* or *Haliotis* (abalone) shells. It has a siphonoplax lined with coarse granules (*Zirfaea* has no siphonoplax) (Evans and Fisher 1966) and can bore into nephrite (Monterey, California, Wilson and Kennedy 1984). *Penitella penita* has a heavy membranous siphonoplax, a calcified callum and a distinctive **mesoplax**. Its anterior rasping surface covers less than half the valve area (Kozloff 1974) (Fig. 1, 3). It can be up to 70 mm in length. *Penitella fitchi* also has a heavy siphonoplax, but has a callum with a gap. This is a rare species, found low in the intertidal up to 25 meters deep. *Penitella turnerae* is larger than *P. penita* (to 125 mm), and less common. It is stout, and like *Zirfaea* lacks a siphonoplax. It has a distinctive, rounded mesoplax, however, and its long, white, retractable

siphons are tipped with solid red. Like *Zirfaea*, it has a strongly angled anterior ventral edge, but unlike *Zirfaea*, *P. turnerae* has a callum. *Penitella richardsoni* (= *gabbi*, Kennedy 1989) is also small (up to 75 mm) with a warty, creamy-lemon colored siphon and it is not common. It is different from the other members of this genus as its umbone reflection is not appressed to the anterior end, a character also found in *C. ovoidea*. *Penitella richardsoni* differs from *C. ovoidea* by having a callum that does not gap and a more elongated shell (Coan and Valentich-Scott 2007). A new species of *Penitella*, *P. hopkinsi*, was described from Alaska, but it not yet reported in our area (Kennedy and Armentrout 1989). With adult specimens, it should be easy to tell *Penitella* from *Zirfaea* because the latter species has a long, non-retractable siphon and a membranous covering of the anterior, instead of a calcareous callum. Small shells without the callum could be young *Penitella* as well as mature *Zirfaea* and size at maturity varies greatly with environmental condition.

Ecological Information

Range: Type locality is San Diego, California (Turner 1955). Eastern Pacific distribution includes the Gulf of Alaska (e.g., Chirikof Island) to Pequena, Baja California. The first presence of *P. penita* in the fossil record is in the Oligocene in California (for pholad palaeoecology see Kennedy 1974, 1993) and fossil pholad beds can be observed at 2–15 meters above the high tide line on cliffs in Coos Bay and southward (Evans 1968d).

Local Distribution: Coos Bay distribution at Pigeon Point, Fossil Point, and Coos Head. Other Oregon sites include Yaquina and Netarts Bays (Turner 1955).

Habitat: Individuals found in open coast habitats as well as exposed bays (Haderlie and Abbott 1980), where they bore into mud and rock and prefer northeast surfaces, where algae and light are reduced (similar to barnacles). The ability of *P. penita* to utilize a wide variety of substrates leads to the wide geographic distribution (Evans 1968d). Harder substrates produce individuals with heavier, less elongate shells and larger muscles (Evans and LeMessurier 1972). The substrate also affects the burrowing speed, as harder rock leads to individuals that burrow and grow more slowly. For example,

individuals in soft rock may mature (and stop burrowing) at three years, while those in harder rock may mature as late as 21 years. Such timing corresponds to burrowing speeds that are 4 (hard substrate) to 50 mm (soft substrate)/year (Haderlie and Abbott 1980). Substrate type (e.g., hard versus soft) has been shown to alter the piddock shell shape, size and hardness (Evans 1968c; Tajima and Kondo 2003). Piddock burrows have the ability, particularly when individuals are present in large numbers, of compromising the stability of shorelines throughout their lifetimes (e.g., *Pholas dactylus*, *Barnea candida*, *B. parva*, Pinn et al. 2005; Davidson and de Rivera 2012). The ability of *P. penita* to burrow into a variety of substrates (e.g., clay, sandstone, cement, Coan and Valentich-Scott 2007) renders it a significant species in the erosion and destruction of marine structures (e.g., jetties). For example, erosion from physical factors leads to roughly 0.5 mm substrate eroded/year while that due to erosion from *P. penita* is 12 mm/year (Fossil Point, Coos Bay, Evans 1968a).

Salinity: Collected at salinities of 30.

Temperature: Cold to temperate waters.

Tidal Level: Intertidal and subtidal (Evans 1967), with a broad distribution vertically, individuals are found as high as +0.6 m (Coos Bay, Evans 1968a) and as low as -91 m (Kofoid and Miller 1927).

Associates: Other nestling and burrowing invertebrates utilize the burrows of *Penitella penita* (e.g. polychaetes *Thelepus*, *Halosydna*, clams *Hiatella*, *Entodesma*, *Zirfaea*, Coos Bay, Table 2, Evans 1967).

Abundance: Often co-occurs with other pholads (e.g., *Zirfaea pilsbryi*, *Penitella* spp., *Netastoma rostratum*) (Haderlie 1979). In Oregon, *Penitella penita* accounted for up to 90% of all boring species in the low intertidal and has been called the most common and widely distributed rock boring clam in the eastern Pacific (Evans 1968d). However, in California, *P. penita* was less abundant than the congeners, *P. conradi* and *P. richardsoni* (Haderlie and Abbott 1980). Fossil records (El Rosario, Baja California) suggest densities as high as 200 individuals/m² (Ledesma-Vazquez and Johnson 1994).

Life-History Information

Reproduction: Reproductive strategies are variable among the Pholadidae (e.g.,

reproduction in *Barnea candida* includes hermaphroditic, dioecious, oviparous and larviparous, Evans 1970). *Penitella penita* is dioecious and oviparous. Sexual maturity is postponed until growth stops (Evans 1970), as individuals become sexually mature once callum is formed and their foot atrophies (Haderlie and Abbott 1980). Gonad morphology in mature individuals suggests gamete development in February, ripe gametes in June and spawning in July (Fossil Point, Coos Bay, Evans 1970). The development of *P. penita* has not yet been described. Boyle and Turner (1976) described the reproduction and development of the east coast pholad, *Martesia striata*. This species spawns in February and eggs are translucent white and 45–46.8 µm in diameter (33°C, Turner and Johnson 1968; 21°C, Boyle and Turner 1976).

Larva: Bivalve development, including members of the Pholadidae, generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. However, in the deep water pholad genus, *Xylophaga*, species brood larvae until late veliger stages (Kennedy 1974; Voight 2009). Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the “D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone. Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig. 1, Kabat and O’Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001.) Larvae of *P. penita* are free swimming with a pelagic duration of two weeks (Haderlie and Abbott 1980) with peaks in settlement occurring from August to September (Evans 1970). The development of other pholads (e.g. *Barnea truncata*, Chanley 1965; *Cyrtoleura costata*, Chanley and Andrews 1971; *Martesia striata*, Boyle and Turber

1976) proceeds as planktotrophic veliger larvae. After 24 hours, *M. striata* larvae are straight hinge veligers (68 µm in length and 59 µm in height, Boyle and Turner 1976). After eight days, they are umbo larvae (129–224 µm) and they are pediveligers by 28–32 days (224–236 µm) post fertilization. Metamorphosis in *M. striata* occurs after 48–53 days (see Table 1, Figure 1, Boyle and Turner 1976). (see also Campos and Ramorino 1990 for planktonic pholad larvae from Chile).

Juvenile: Average time to maturity is 33 months and metamorphosis is marked by the resorption of the foot (Evans 1968a, 1970). This species is unusual in having determinate growth where, at about three years, individuals metamorphose into non-boring adults (about 55 mm in length). Crowding may induce early metamorphosis (Evans 1968d). Anterior end of juveniles is soft (without callum), while animal is actively burrowing. Exposed foot is circular and has developed as a suction disc (Fig. 5).

Longevity: Lives until substrate surrounding the burrow erodes enough to make it subject to predators. Longevity is thus dependent on erosion rate and varies with rock hardness (Haderlie and Abbott 1980). At Fossil Point, erosion process takes about six years following metamorphosis (nine years total lifespan, Evans 1970).

Growth Rate: Once they settle, growth proceeds at a rate of 22 growth bands/year (Haderlie and Abbott 1980). Growth occurs in two distinct phases: the first where individuals are actively boring and growing, and the second where both boring and growth stops (Evans 1970).

Food: A suspension feeder, *P. penita* uses long siphons and gills to filter food.

Predators: Flatworms *Stylochoplana*, *Notoplana inquieta*, where worms enter the shell, eat the flesh, and lay eggs (Evans 1967). Additionally, interference from *Botula californiensis*, which settles on the burrow entrance may lead to the death of *P. penita* individuals (Evans 1967). Other invertebrates predators include *Ceratostoma foliatum*, *Roperia poulsoni* (Haderlie and Abbott 1980).

Behavior: Pholads are the most efficient burrowers of the seven families of rock-boring bivalves (Evans 1968a). Grinding is assisted by keeping algae out of burrow with sea water, by loosening rock grains, and by ciliary

currents which flush out cavity (Keen 1971). The callum shape is determined by the contours of the burrow and, in artificial burrows, the callum can be rather square (versus pear-shaped, Haderlie 1981b).

Bibliography

1. BOYLE, P. J., and R. D. TURNER. 1976. Larval development of wood boring piddock *Martesia striata* (L.) (Mollusca: Bivalvia: Pholadidae). *Journal of Experimental Marine Biology and Ecology*. 22:55-68.
2. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
3. CAMPOS, B., and L. RAMORINO. 1990. Larvae and postlarvae of Pholadacea from Chile (Mollusca, Bivalvia). *Revista de Biología Marina*. 25:15-64.
4. CHANLEY, P. E. 1965. Larval development of a boring clam, *Barnea truncata*. *Chesapeake Science*. 6:162-166.
5. CHANLEY, P. E., and J. D. ANDREWS. 1971. Aids for identification of bivalve larvae of Virginia. *Malacologia*. 11:45-119.
6. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
7. DAVIDSON, T. M., and C. E. DE RIVERA. 2012. Per capita effects and burrow morphology of a burrowing isopod (*Sphaeroma quoianum*) in different estuarine substrata. *Journal of Crustacean Biology*. 32:25-30.
8. EVANS, J. W. 1967. Relationship between *Penitella penita* (Conrad, 1837) and other organisms of the rocky shore. *The Veliger*. 10:148-151.
9. —. 1968a. Factors modifying the morphology of the rock-boring clam, *Penitella penita* (Conrad, 1837). *Journal of Molluscan Studies*. 38:111-119.
10. —. 1968b. Growth rate of the rock-boring clam *Penitella penita* (Conrad 1837) in relation to hardness of rock and other factors. *Ecology*. 49:619-628.
11. —. 1968c. The effect of rock hardness and other factors on the shape of the burrow of the rock-boring clam *Penitella penita* (Conrad 1837) (Family Pholadidae). *Palaeogeography, Palaeoclimatology, Palaeoecology*. 4:271-278.
12. —. 1968d. The role of *Penitella penita* (Conrad 1837)(Family Pholadidae) as eroders along the Pacific coast of North America. *Ecology*. 49:156-159.
13. —. 1970. Sexuality in rock-boring clam *Penitella penita* (Conrad 1837). *Canadian Journal of Zoology*. 48:625-627.
14. EVANS, J. W., and D. FISHER. 1966. A new species of *Penitella* (family Pholadidae) from Coos Bay, Oregon. *The Veliger*. 8:222-224.
15. EVANS, J. W., and M. H. LEMESSURIER. 1972. Functional micromorphology and circadian growth of the rock-boring clam *Penitella penita*. *Canadian Journal of Zoology*. 50:1251-1258.
16. HADERLIE, E. C. 1979. Range extension for *Penitella fitchi* Turner, 1955 (Bivalvia, Pholadidae). *Veliger*. 22:85-85.
17. —. 1981a. Growth rates of *Penitella penita* (Conrad, 1837), *Chaceia ovoidea* (Gould, 1851)(Bivalvia, Pholadidae) and other rock boring bivalves in Monterey Bay. *Veliger*. 24:109-114.
18. —. 1981b. Influence of terminal end of burrow on callum shape in the rock boring clam *Penitella penita* (Conrad, 1837)(Bivalvia, Pholadidae). *Veliger*. 24:51-53.
19. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
20. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine*

- invertebrates of the northern Pacific Coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
21. KEEN, A. M. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. Stanford University Press, Stanford, CA.
 22. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
 23. KENNEDY, G. L. 1974. West American Cenozoic Pholadidae. *Memoirs of the San Diego Society of Natural History*. 8:1-128.
 24. —. 1989. Status of *Penitella gabbii* (Tryon, 1863) in the Eastern and Western Pacific, and description of the previously misidentified Eastern Pacific species (Bivalvia, Pholadidae). *Veliger*. 32:313-319.
 25. —. 1993. New Cretaceous and Tertiary Pholadidae (Mollusca, Bivalvia) from California. *Journal of Paleontology*. 67:397-404.
 26. KENNEDY, G. L., and J. M. ARMENTROUT. 1989. A new species of chimney-building *Penitella* from the Gulf of Alaska (Bivalvia, Pholadidae). *Veliger*. 32:320-325.
 27. KOFOID, C. A., and R. C. MILLER. 1927. Biological section, p. 188-343. *In: Marine Borers and their Relation to Marine Construction on the Pacific Coast*. Final Report of the San Francisco Bay Marine Piling Committee, San Francisco, Final Report of the San Francisco Bay Marine Piling Committee, San Francisco.
 28. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
 29. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 30. LEDESMA-VAZQUEZ, J., and M. E. JOHNSON. 1994. Late pliocene abrasion platform from the Cantil Costero formation of Baja California. *Ciencias Marinas*. 20:139-157.
 31. LLOYD, F. E. 1896. On *Pholadidea penita*, and its method of boring. *Science*. iv:188-190.
 32. MARSHALL, B. A., and H. G. SPENCER. 2013. Comments on some taxonomic changes affecting marine bivalvia of the New Zealand region recently introduced in Huber's *Compendium of Bivalves*, with some additional taxonomic changes. *Molluscan Research*. 33:40-49.
 33. PINN, E. H., C. A. RICHARDSON, R. C. THOMPSON, and S. J. HAWKINS. 2005. Burrow morphology, biometry, age and growth of piddocks (Mollusca: Bivalvia: Pholadidae) on the south coast of England. *Marine Biology*. 147:943-953.
 34. REFT, A. J., and J. R. VOIGHT. 2009. Sensory structures on the siphons of wood-boring bivalves (Pholadidae: Xylophaginae: *Xylophaga*). *Nautilus*. 123:43-48.
 35. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides: an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
 36. TAJIMA, T., and Y. KONDO. 2003. The relationship between functional shell morphology and nature of the bored substratum in the family Pholadidae (Bivalvia). *Fossils (Tokyo)*:5-19.
 37. TURNER, R. D. 1955. The family Pholadidae in the western Atlantic and the eastern Pacific. II. Martesiinae, Jouannetiinae and Xylophaginae. *Johnsonia (Harvard University)*. 3:65-160, 80-85.
 38. TURNER, R. D., and A. C. JOHNSON. 1968. Biology of marine wood-boring mollusks, p. 259-301. *In: Marine borers, fungi and fouling organisms of wood*. E. B. G. Jones and S. K. Eltringham (eds.). Organization for

Economic Cooperation and
Development, Paris.

39. VOIGHT, J. R. 2009. Diversity and reproduction of near-shore vs offshore wood-boring bivalves (Pholadidae: Xylophaginae) of the deep eastern Pacific Ocean, with three new species. *Journal of Molluscan Studies*. 75:167-174.
40. WILSON, E. C., and G. L. KENNEDY. 1984. The boring clam, *Penitella conradi*, (Bivalvia: Pholadidae) in nephrite from Monterey County, California. *Nautilus*. 98:159-162.

Updated 2015

Zirfaea pilsbryi

The rough piddock

Phylum: Mollusca
Class: Bivalvia; Heterodonta
Order: Myoida
Family: Pholadidae

Taxonomy: The taxonomies of both pholad species in this guide (*Z. pilsbryi* and *Penitella penita*) are extensive and complicated, including many synonyms and overlapping descriptions (for full list of synonymies see Kennedy 1974). *Zirfaea pilsbryi* was originally described as *Z. gabbii*, a species eventually moved to the genus *Penitella* (see *P. gabbii*, Kennedy 1974). Lowe renamed and described *Z. pilsbryi* in 1931. Thus, these three species names (*Z. pilsbryi*, *Z. gabbii*, and *P. gabbii*) and the subspecies designation, *Z. gabbii femii* (Adegoke 1967 in Kennedy 1974), are common synonyms, with descriptions that overlap and are specific to original author (see Kennedy 1974).

Description

Size: Individuals up to 150 mm in length (Ricketts and Calvin 1971; Haderlie and Abbott 1980; Kozloff 1993) and may be the largest of the boring species (Ricketts and Calvin 1971). Coos Bay (Fossil Point) specimens were approximately 75–125 mm long.

Color: White exterior, interior also white or light salmon (Turner 1954; Haderlie and Abbott 1980). Siphons gray-white to ivory, speckled with very small (1.5–2 mm) orange chitinous spots, dark red around siphonal openings and incurrent cirri (Fig. 1). Foot and mantle are ivory in color, when preserved (Turner 1954). Periostacrum is dark brown (Haderlie and Abbott 1980).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Myoid bivalves are burrowers and borers, with long siphons and hinges with few teeth (Coan and Valentich-Scott 2007). Members of the Pholadidae bore into a variety of substrates, possess no pallets on siphon tips and have an anterior end that is pointed or curved with no notch (contrast to Teredinidae species, e.g., *Bankia setacea*, this guide) (see Plate 427F, 430D, Coan and

Valentich-Scott 2007). While most pholad species are intertidal or subtidal, some can be found boring into wood at great depths (e.g., 7,250 meters *Xylophaga*, Kennedy 1974; Reft and Voight 2009; Voight 2009; Marshall and Spencer 2013).

Body: (see Plate 297, Ricketts and Calvin 1952; Fig 361, Kozloff 1993).

Color:

Interior:

Exterior:

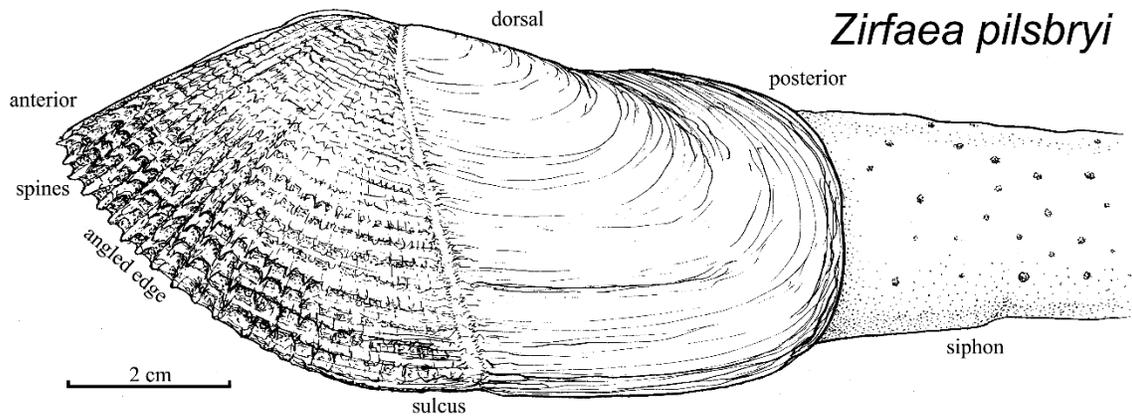
Byssus:

Gills:

Shell: Gapes widely at both ends and valves have ventral marginal groove (Fig. 2). Anterior end has rasping ridges, but posterior is with smooth, concentric lines (Haderlie and Abbott 1980; Kozloff 1993). Anterior end of shell is not as prominently demarcated from the posterior (compare to *Penitella penita*, this guide). Shell is relatively fragile as it gains ample protection from its surrounding burrow (Ricketts and Calvin 1952).

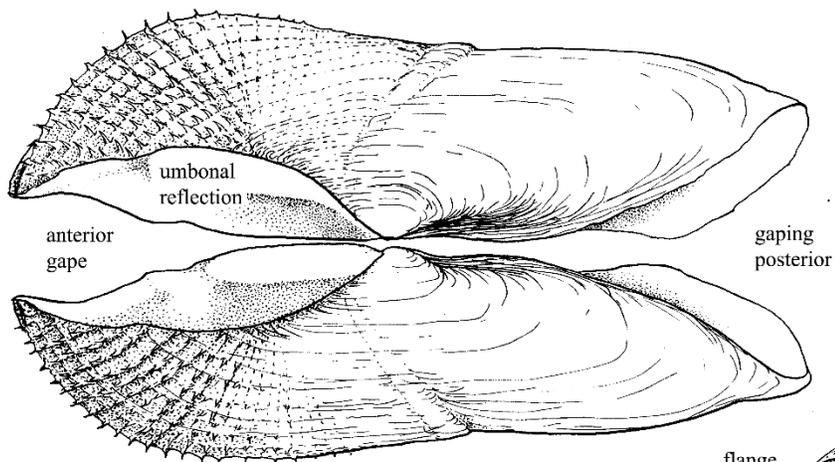
Interior: The groove separating anterior and posterior sections of valve (or umbonal ventral sulcus) is conspicuous in juveniles, but almost disappears near ventral margin in older specimens (Kennedy 1974) (Fig. 1). Strong muscle scars present, but no hinge or ligament (Pholadidae, Quayle 1970). Pallial sinus is broad and deep, extending nearly to umbo (Fig. 3). The apophysis (or myophore) is broad, with rounded spoon-shaped end (Fig. 3).

Exterior: Shape hard, solid, elongate, oval, but not globose. Valves divided into two regions: anterior triangular and posterior is rounded with concentric rings (Fig. 1). Anterior is triangular with rough file-like radial and concentric denticulations, which can project into spines on anterior margin (Fig. 1). Rasping portion covers half total valve area (Kozloff 1993). No callum is present (calcareous anterior accessory plate, see *Penitella penita*, this guide), only a protective membrane. Umbonal reflection is wide. The anterior ventral edge of valve is strongly angled (Fig. 1). The posterior portion is with

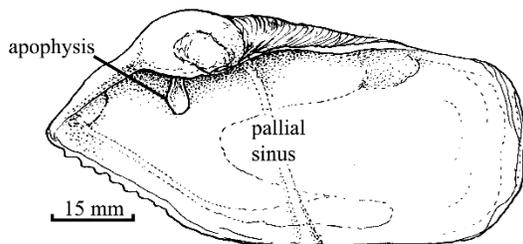


1. *Zirfaea pilsbryi* (L:93mm) x1.5:

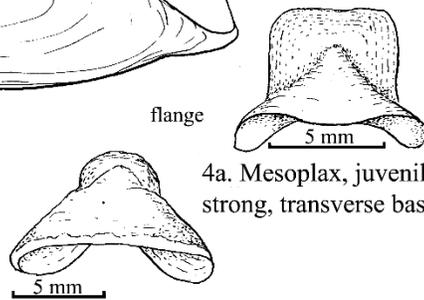
elongate shell divided by umbonal ventral sulcus into anterior: triangular rasping surface, spined angled edge without callum; posterior truncate, with concentric striations only; siphons long, not retractible, with small chitinous patches.



2. (Dorsal view).



3. Interior, right valve x1:
pallial sinus broad, deep;
apophysis spoon-shaped.



4a. Mesoplax, juvenile x5.5:
strong, transverse basal flange.

4b. Mesoplax, adult x3.5:
flange obscure (Turner, 1954).

concentric striations only and is rounded to truncate (Fig. 1). Gapes extend to the middle of the shell (Keen and Coan 1974).

Hinge:

Eyes:

Foot: Foot is round and truncate (Turner 1954).

Siphons: Fused and very long (6–8 times the shell length) and can extend 15 cm above the burrow surface (Haderlie and Abbott 1980). They are non-retractible and covered with small chitinous discs, but without papillae or pustules. No siphonoplax (flaps around siphon, see *Penitella penita*, this guide). Periostracum extends from over 1/3 shell posterior to cover part of siphons (Quayle 1970).

Burrow: *Zirfaea pilsbryi* burrows into heavy mud, clay and shale to 50 cm depths. The foot is sucker-like and attaches to the substrate so that the shell can rotate slowly and create a cylindrical burrow. Shell valves rock back and forth by contractions of anterior and posterior adductor muscles. Individuals rotate after each stroke, making a cylindrical burrow. While burrowing, individuals exude particles out the inhalant siphon by contracting their body quickly (Ricketts and Calvin 1952; Haderlie and Abbott 1980). Thirty-two movements make for one entire revolution, which takes a total of 70 minutes and after each revolution, the rotating direction alternates (MacGinitie in Ricketts and Calvin 1952). Burrows may be pear-shaped (producing *Gastrochaenolites*-type traces, Furlong et al. 2014) rather than cone-shaped, and individuals often do not fit as tightly within their burrows as other pholads (Evans and Fisher 1966). (see also **Habitat and Behavior.**)

Pholadidae-specific character

Mesoplax: There is only one mesoplax (or small accessory dorsal plate) present in this species. It is weak and reduced (Evans and Fisher 1966) and with a transverse basal flange that well-developed in juvenile (Fig. 4a), but becomes less obvious in adults (Fig. 4b). (Note: the mesoplax is often lost in collecting.)

Possible Misidentifications

There are several families of burrowing clams and the Pholadidae can be distinguished by their distinctively marked body areas.

Members of the Teredinidae and Pholadidae can be found locally. They can be distinguished by the absence of pallets on siphon tips in the latter family as well as an anterior end that is not notched, as in the Teredinidae. The Pholadidae includes 10 species locally, within the following genera: *Barnea* (*B. subtruncata*), *Chaceia* (*C. ovoidea*), *Netastoma* (*N. rostratum*), *Parapholas* (*P. californica*), *Penitella* (five local species) and *Zirfaea* (*Z. pilsbryi*). The genus *Zirfaea* is characterized by adults that burrow into sand or mud, the absence of a callum in mature individuals, and a shell sculpture that is divided into two distinct zones (see Plates 427C, 429D, Coan and Valentich-Scott 2007). The genus *Barnea*, for example, also lacks a callum, but does not have these two distinct zones. All other local genera are characterized by the presence of a callum and all except *Netastoma* have a myopore as well. *Parapholas* species have shell sculpture with three distinct zones, where members of *Chaceia* and *Penitella* have two.

The genus closest to *Zirfaea*, and most likely to be confused with it, is *Penitella*. As mentioned above, *Penitella*'s valves are also divided into two distinct sections, but it differs in having a calcareous anterior callum, or accessory plate (in the adult) as well as a posterior which gapes only at the end, not to the middle of the shell (it has no anterior gape) and the apophysis is narrow, not broad. No *Penitella* species has a siphon longer than its body (Evans and Fisher 1966) and all *Penitella* species have retractable siphons. There are five species of *Penitella* in our area (see Coan and Valentich-Scott 2007).

Penitella conradi is very small and is found in *Mytilus* or *Haliotis* (abalone) shells. It has a siphonoplax lined with coarse granules (*Zirfaea* has no siphonoplax) (Evans and Fisher 1966) and can bore into nephrite (Monterey, California, Wilson and Kennedy 1984). *Penitella penita* (see description in this guide) has a heavy membraneous siphonoplax, a calcified callum and a distinctive **mesoplax**. Its anterior rasping surface covers less than half the valve area (Kozloff 1974). It can be up to 70 mm in length. *Penitella fitchi* also has a heavy siphonoplax, but has a callum with a gap. This is a rare species, found low in the intertidal and up to 25 meters deep. *Penitella*

turnerae is larger than *P. penita* (to 125 mm), and less common. It is stout, and like *Zirfaea* lacks a siphonoplax. It has a distinctive, rounded mesoplax, however, and its long, white, retractable siphons are tipped with solid red. Like *Zirfaea*, it has a strongly angled anterior ventral edge, but unlike *Zirfaea*, *P. turnerae* has a callum. *Penitella richardsoni* (= *gabbi*, Kennedy 1989) is also small (up to 75 mm) with a warty, creamy-lemon colored siphon and it is not common. It is different from the other members of this genus as its umbone reflection is not appressed to the anterior end, a character also found in *C. ovoidea*. *Penitella richardsoni* differs from *C. ovoidea* by having a callum that does not gap and an more elongated shell (Coan and Valentich-Scott 2007). A new species of *Penitella*, *P. hopkinsi*, was described from Alaska, but it not yet reported in our area (Kennedy and Armentrout 1989). With adult specimens, it should be easy to tell *Zirfaea* from *Penitella* by its long, non-retractable siphon and by the membranous covering of the anterior, instead of a calcareous callum. Small shells without the callum could be young *Penitella* as well as mature *Zirfaea* and size at maturity varies greatly with environmental condition.

Zirfaea crispata is a small Atlantic species without chitinous spots on the siphons. It may have been introduced into Humboldt Bay, California with eastern oyster spat *Crassostrea* (Turner 1954), but is not currently included in local intertidal guides (see Coan and Valentich-Scott 2007).

Ecological Information

Range: Type locality is Bolinas Bay, California (Turner 1954). Eastern Pacific distribution includes the Bering Sea to Baja, California (Ricketts and Calvin 1952; Haderlie and Abbott 1980). *Zirfaea pilsbryi* is the most common fossil pholidid on the Pacific coast and dates from the Pleistocene in California and northern Baja California (for pholid palaeoecology see Kennedy 1974, 1993).

Local Distribution: Coos Bay distribution at South Slough, Fossil Point, Tillamook Bay, Netarts Bay, Yaquina Bay (Turner 1954) and Siuslaw River (Hancock et al. 1979).

Habitat: *Zirfaea pilsbryi* bores into shale, clay, sand or mud, as soft rock, to depth of 25–35 cm (Turner 1954), where mud and clay are preferred substrates (Coan and Valentich-

Scott 2007), but individuals are sometimes seen in outside rocky reefs (Ricketts and Calvin 1952). In one case, individuals were seen burrowing into wood (Emerson 1951). Substrate type (e.g., hard versus soft) has been shown to alter the piddock shell shape, size and hardness (see Tajima and Kondo 2003). Piddock burrows have the ability, particularly when individuals are present in large numbers, of compromising the stability of shorelines throughout their lifetimes (e.g., *Pholas dactylus*, *Barnea candida*, *B. parva*, Pinn et al. 2005).

Salinity:

Temperature: Cold to temperate waters.

Tidal Level: Intertidal to deep water (Quayle 1970), below -0.3 meters (Kozloff 1993)

Associates: Associates include other nestling and burrowing clams (e.g., *Penitella*, *Hiatella*, *Entodesma*, *Adula*) as well as the commensal pea crab, *Opisthopus transversus*, and the flat-worm *Cryptophallus magnus* (MacGinitie 1935; Haderlie and Abbott 1980).

Abundance: Can be quite dense in locally suitable conditions. This species is the third most abundant pholid at Fossil Point, Coos Bay (following *Penitella penita*, *P. richardsoni*, Evans and Fisher 1966).

Life-History Information

Reproduction: Spawning occurred in July in southern California (MacGinitie 1935), but little is known about the reproduction and development of this species. Breeding occurs in the congener, *Z. crispata*, in from March through October (Northumberland coast, United Kingdom, Allen 1969). Boyle and Turner (1976) described the reproduction and development of the east coast pholid, *Martesia striata*. This species spawns in February and eggs are translucent white and 45–46.8 µm in diameter (33°C, Turner and Johnson 1968; 21°C, Boyle and Turner 1976).

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. However, in the deep water pholid genus, *Xylophaga*, species brood larvae until late veliger stages (Kennedy 1974; Voight 2009). Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the

larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the “D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone. Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (Kabat and O’Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001). Larvae of the common, local pholad, *P. penita*, are free swimming with a pelagic duration of two weeks (Haderlie and Abbott 1980). The development of other pholads (e.g., *Barnea truncata*, Chanley 1965; *Cyrtopleura costata*, Chanley and Andrews 1971; *Martesia striata*, Boyle and Turber 1976) proceeds as planktotrophic veliger larvae. After 24 hours, *M. striata* larvae are straight hinge veligers (68 µm in length and 59 µm in height, Boyle and Turner 1976). After eight days, they are umbo larvae (129–224 µm) and they are pediveligers by 28–32 days (224–236 µm) post fertilization. Metamorphosis in *M. striata* occurs after 48-53 days (see Table 1, Figure 1, Boyle and Turner 1976). (see also Campos and Ramorino 1990 for planktonic pholad larvae from Chile). The development of *Z. subconstricta* was followed by Ito (2005) where D-stage larvae were 70 µm in length and 60 µm in height and later stages were uniformly round and 150–200 µm in diameter. Metamorphosis occurred after five weeks and shells became asymmetrical once individuals were approximately 320 µm (see Fig. 1, Ito 2005).

Juvenile:

Longevity: 7–8 years (MacGinitie and MacGinitie 1947; Ricketts and Calvin 1952). The lifespan of the congener, *Z. crispata* is 5–7 years (Allen 1969).

Growth Rate: Animals grow throughout their entire life, unlike *Penitella* species (see **Behavior**). Growth rate of the congener, *Z. crispata*, is 8 mm/year (Allen 1969).

Food: A suspension feeder, *Z. pilsbryi* uses its inhalant siphon to filter food through very large gills that extend into the exposed siphon (Haderlie and Abbott 1980).

Predators: Flatworms.

Behavior: *Zirfaea pilsbryi* is unusual among pholads for its indeterminate growth, as an individual remains an active burrower for its entire life and does not stop and seal its shell with a callum when mature (MacGinitie 1935).

Bibliography

1. ALLEN, J. A. 1969. Observations on size composition and breeding of Northumberland populations of *Zirphaea crispata* (Pholadidae: Bivalvia). *Marine Biology*. 3:269-275.
2. BOYLE, P. J., and R. D. TURNER. 1976. Larval development of wood boring piddock *Martesia striata* (L.) (Mollusca: Bivalvia: Pholadidae). *Journal of Experimental Marine Biology and Ecology*. 22:55-68.
3. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
4. CAMPOS, B., and L. RAMORINO. 1990. Larvae and postlarvae of Pholadacea from Chile (Mollusca, Bivalvia). *Revista de Biología Marina*. 25:15-64.
5. CHANLEY, P. E. 1965. Larval development of a boring clam, *Barnea truncata*. *Chesapeake Science*. 6:162-166.
6. CHANLEY, P. E., and J. D. ANDREWS. 1971. Aids for identification of bivalve larvae of Virginia. *Malacologia*. 11:45-119.
7. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
8. EMERSON, W. K. 1951. An unusual habitat for *Zirfaea pilsbryi* (Mollusca: VIADER). *Bulletin of the Southern California Academy of Sciences*. 50:89-91.
9. EVANS, J. W., and D. FISHER. 1966. A new species of *Penitella* (family Pholadidae) from Coos Bay, Oregon. *The Veliger*. 8:222-224.
10. FURLONG, C. M., M. K. GINGRAS, and J. ZONNEVELD. 2015.

- Trypanites-type ichnofacies at the Bay of Fundy, Nova Scotia, Canada. *Palaios*. 30:258-271.
11. HADERLIE, E. C. 1980. Stone boring marine bivalves from Monterey Bay, California. *Veliger*. 22:345-354.
 12. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 13. HANCOCK, D. R., T. F. GAUMER, G. B. WILLEKE, G. P. ROBART, and J. FLYNN. 1979. Subtidal clam populations: distribution, abundance, and ecology. Oregon State University, Sea Grant College Program, Corvallis.
 14. ITO, Y. 2005. Functional shell morphology in early developmental stages of a boring bivalve *Zirfaea subconstricta* (Pholadidae). *Paleontological Research*. 9:189-202.
 15. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 16. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
 17. KENNEDY, G. L. 1974. West American Cenozoic Pholadidae. *Memoirs of the San Diego Society of Natural History*. 8:1-128.
 18. —. 1989. Status of *Penitella gabbii* (Tryon, 1863) in the Eastern and Western Pacific, and description of the previously misidentified Eastern Pacific species (Bivalvia, Pholadidae). *Veliger*. 32:313-319.
 19. —. 1993. New Cretaceous and Tertiary Pholadidae (Mollusca, Bivalvia) from California. *Journal of Paleontology*. 67:397-404.
 20. KENNEDY, G. L., and J. M. ARMENTROUT. 1989. A new species of chimney-building *Penitella* from the Gulf of Alaska (Bivalvia, Pholadidae). *Veliger*. 32:320-325.
 21. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
 22. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 23. MACGINITIE, G. E. 1935. Ecological aspects of a California marine estuary. *American Midland Naturlist*. 16:629-765.
 24. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 25. MARSHALL, B. A., and H. G. SPENCER. 2013. Comments on some taxonomic changes affecting marine bivalvia of the New Zealand region recently introduced in Huber's Compendium of Bivalves, with some additional taxonomic changes. *Molluscan Research*. 33:40-49.
 26. PINN, E. H., C. A. RICHARDSON, R. C. THOMPSON, and S. J. HAWKINS. 2005. Burrow morphology, biometry, age and growth of piddocks (Mollusca: Bivalvia: Pholadidae) on the south coast of England. *Marine Biology*. 147:943-953.
 27. QUAYLE, D. B. 1970. The intertidal bivalves of British Columbia. British Columbia Provincial Museum, Victoria, BC, Canada.
 28. REFT, A. J., and J. R. VOIGHT. 2009. Sensory structures on the siphons of wood-boring bivalves (Pholadidae: Xylophaginae: *Xylophaga*). *Nautilus*. 123:43-48.
 29. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides: an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
 30. —. 1971. Between Pacific tides. Stanford University Press, Stanford, California.

31. TAJIMA, T., and Y. KONDO. 2003. The relationship between functional shell morphology and nature of the bored substratum in the family Pholadidae (Bivalvia). *Fossils* (Tokyo):5-19.
32. TURNER, R. D. 1954. The family Pholadidae in the western Atlantic and the eastern Pacific. Part I. Pholadinae. *Johnsonia*. 3:1-64.
33. TURNER, R. D., and A. C. JOHNSON. 1968. Biology of marine wood-boring mollusks, p. 259-301. *In*: Marine borers, fungi and fouling organisms of wood. E. B. G. Jones and S. K. Eltringham (eds.). Organization for Economic Cooperation and Development, Paris.
34. VOIGHT, J. R. 2009. Diversity and reproduction of near-shore vs offshore wood-boring bivalves (Pholadidae: Xylophaginae) of the deep eastern Pacific Ocean, with three new species. *Journal of Molluscan Studies*. 75:167-174.
35. WILSON, E. C., and G. L. KENNEDY. 1984. The boring clam, *Penitella conradi*, (Bivalvia: Pholadidae) in nephrite from Monterey County, California. *Nautilus*. 98:159-162.

Updated 2015

Bankia setacea

The northwest or feathery shipworm

Phylum: Mollusca
Class: Bivalvia; Heterodonta
Order: Myoida
Family: Teredinidae

Taxonomy: The original binomen for *Bankia setacea* was *Xylotrya setacea*, described by Tryon in 1863 (Turner 1966). William Leach described several molluscan genera, including *Xylotrya*, but how his descriptions were interpreted varied. Although Menke believed *Xylotrya* to be a member of the Pholadidae, Gray understood it as a member of the Terdinidae and synonymized it with the genus *Bankia*, a genus designated by the latter author in 1842. Most authors refer to *Bankia setacea* (e.g. Kozloff 1993; Sipe et al. 2000; Coan and Valentich-Scott 2007; Betcher et al. 2012; Borges et al. 2012; Davidson and de Rivera 2012), although one recent paper sites *Xylotrya setacea* (Siddall et al. 2009). Two additional known synonyms exist currently, including *Bankia osumiensis*, *B. sibirica*.

Description

Size: The largest of the shipworms, with burrows that in one study were found to be up to 15mm in diameter and 1m in length (Haderlie and Mellor 1973). Body size can vary greatly. The illustrated specimen (Fig. 1) is small and has shell diameter of 5 mm.

Color: White with brownish tinges. A long soft whitish tube connects the calcareous shell and pallets (Fig. 1) (Haderlie and Abbott 1980).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Among the bivalves, the Heterodonta are characterized by **ctenidia** that are eulamellibranchiate, fused mantle margins and the presence of long **siphons**. Members of the family Teredinidae are modified for and distinguished by a wood-boring mode of life (Sipe et al. 2000), **pallets** at the siphon tips (see Plate 394C, Coan and Valentich-Scott 2007) and distinct anterior shell indentation. They are commonly called shipworms (though they are not worms at all!) and bore into many wooden structures. The common name

shipworm is based on their vermiform morphology and a shell that only covers the anterior body (Ricketts and Calvin 1952; see images in Turner 1966).

Body: Bizarrely modified bivalve with reduced, sub-globular body. For internal anatomy, see Fig. 1, Canadian...; Fig. 1 Betcher et al. 2012.

Color:

Interior: The auricle (chamber of the heart) is medium sized and rounded. A complex digestion system allows for digestion of wood, which passes from a short esophagus to an alimentary tract to a stomach and finally a caecum where wood is broken down by enzymes (for metabolic compounds see Liu and Townsley 1968, 1970). The caecum is long, blind and has thin walls (Fig. 1, Liu and Townsley 1968).

Exterior:

Byssus:

Ctenidia (Gills): Eulamellibranchiate or filamentous and consisting of two layers on each side of the body. Ctenidia house symbiotic bacteria that synthesize essential nutrients (e.g., amino acids) for the host individual (see **Associates**, Trylek and Allen 1980).

Shell: The two valves gape widely in front of the foot and behind the body (Hill and Kofold 1927; Haderlie and Abbott 1980). Each small valve with three lobes including anterior, median (composed of three separate areas), and posterior, or auricle (Figs. 4a, b, c). In *B. setacea*, the anterior lobe is fairly small, and has many numerous, close-set ridges.

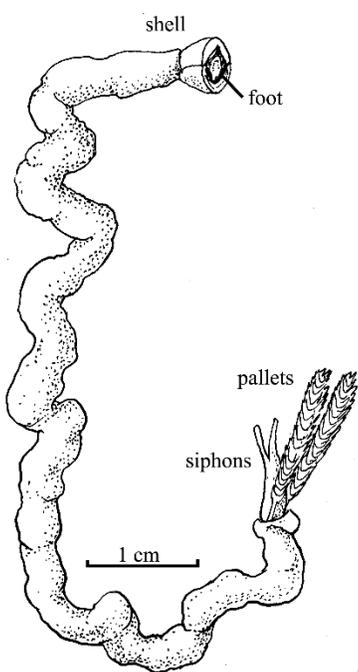
Interior: An internal shell projection for foot attachment or apophysis is present (Fig. 4b) as well as articulating condyles (pivots) on ventral margins (Haderlie and Abbott 1980).

Exterior: Both valves have a file-like exterior surface for rasping wood (Liu and Townsley 1968).

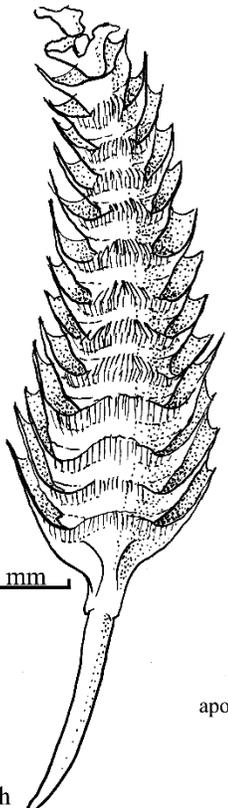
Hinge:

Eyes:

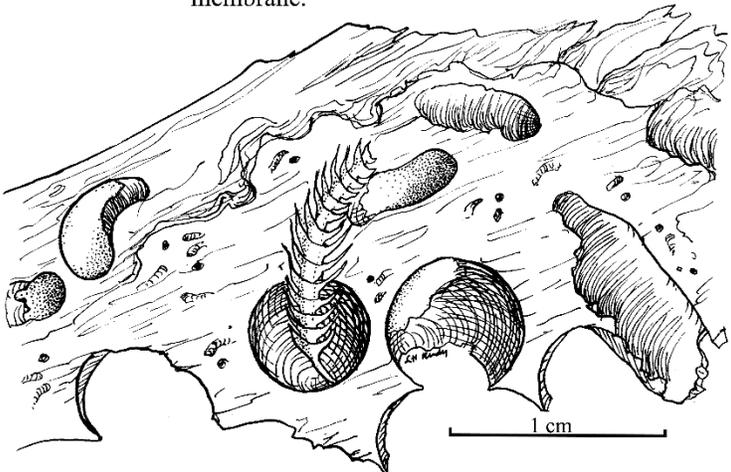
Bankia setacea



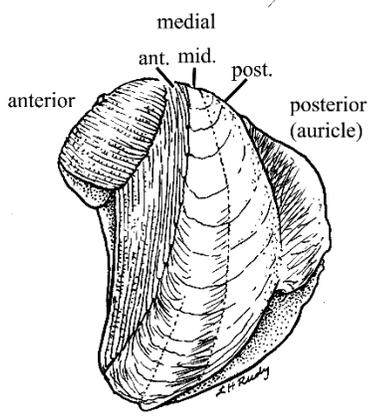
1. *Bankia setacea* (D:5mm) x2:
can be up to 15mm.



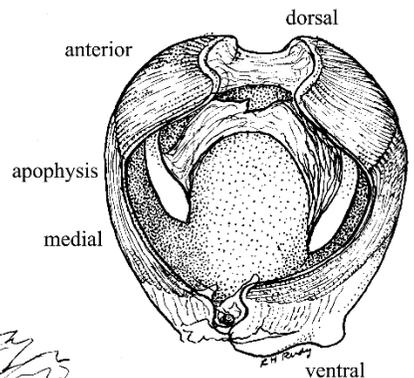
2. Pallet x12:
cone-in-cone segments with
slender projections, connecting
membrane.



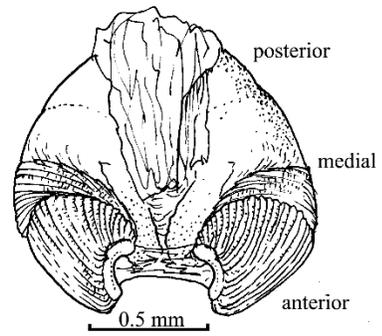
3. Shipworm burrows x4:
several sizes, some calcareous;
pallet of dead animal.



a. Left lateral, showing lobes



b. Frontal



c. Dorsal

4 a.,b.,c., Shell x11.

Foot: Rounded and “sucker-like” (Fig. 1) and allows clam to hold onto wood (Haderlie and Abbott 1980).

Siphons: Elongate (Heterodonta, Myoida, Coan and Valentich-Scott 2007) and used for feeding and respiration (Haderlie and Abbott 1980). Males differ from females in having four rows of papillae (each up to 180 μm in length, see Fig. 14, Quayle 1992) on the exhalant siphon, which is sometimes inserted into female siphon at spawning (Haderlie and Abbott 1980; Kabat and O’Foighil 1987). The tip of the inhalant siphon is surrounded by a crown of six short tentacles (no tentacles are present on the exhalant siphon) (Quayle 1992).

Burrow: Sinuous and revealing pattern of shell’s external grinding surface. Calcareous tube that is produced when individuals stop boring is sometimes apparent (see Fig. 53, Kozloff 1993). Individuals burrow deep into wooden structures, not just along surface (Haderlie and Mellor 1973) and prefer horizontal surfaces along the mudline (Walden et al. 1967). Burrowing is accomplished by alternating contractions of adductor muscles, rocking the clam and toothed valves back and forth. The burrow itself becomes cylindrical as the body of the clam slowly rotates as it burrows (Fig. 3) (Haderlie and Abbott 1980). Burrows can be up to a meter long, with burrowing rate from 43–74 mm per month (Haderlie and Abbott 1980).

Teredinidae-specific character

Pallets: Two calcareous, feather-like structures, attached to the posterior end under a fleshy collar (Figs. 1, 2). These pallets are used to close the burrow when animal is disturbed. They are symmetrical, compound, elongated, blade-like structures and consist of cone-shaped segments (Fig. 2). They are paired, Y-shaped and stacked such that the smallest and oldest pallet is most distal from the individual’s body (Fig. 10, Quayle 1992). Pallets may be extracted from and visualized in dead animals (Hill and Kofold 1927).

Possible Misidentifications

Bivalve classification largely is based on ten characters (Myoida, Coan and Valentich-Scott 2007): morphology of ctenidia, shell interior and exterior, foot, byssus, adductor muscles

and stomach; mode of life (e.g., burrowing); degree of mantle edge fusion; shell mineralogy; molecular phylogenetics. Within the Heterodonta, species have ctenidia that are eulamellibranchiate, mantle margins that are fused and elongated siphons. This group consists of the orders Veneroida, Pholadomyoida and the Myoida. Veneroids have well-developed hinge teeth, the Pholadomyoida are burrowers with thin shells and reduced or absent hinge teeth. The Myoida, to which *B. setacea* belongs, are burrowers and borers, with few hinge teeth. There are four local families including Myidae, Corbulidae, Pholadidae and Teredinidae.

The Teredinidae can be distinguished from other myoid families as wood borers with distinct pallets (Fig. 2) at siphon tips and anterior shell indentations. There are only three local species and *B. setacea* is easily recognized as the only species with pallets that have an elongate, Y-shaped blade and cone-shaped segments. The remaining two species have pallets that are not segmented (Kozloff 1993; Coan and Valentich-Scott 2007).

Teredo navalis, the common and cosmopolitan shipworm, was introduced to San Francisco around 1910 (Hill and Kofold 1927). *Teredo navalis* has simple, spade-shaped pallets, without the separate conical elements of *B. setacea*. *Teredo navalis* also causes more damage to wooden structures than *B. setacea*, being much more adaptable to extremes of temperature and salinity. It is usually much smaller than *B. setacea* and its burrows are nearer the surface. Another introduced species, *Lyrodus pedicellatus*, occurs locally and differs from *T. navalis* by having more periostracum covering the distal half of the pallet, rather than a pallet that is almost entirely calcareous (Coan and Valentich-Scott 2007). *Lyrodus pedicellatus* also has narrower pallets than *T. navalis* (Quayle 1992). Other *Bankia* species are warm water animals, and do not range north of San Diego (Hill and Kofold 1927).

Ecological Information

Range: Type locality is San Francisco Bay, California (Turner 1966). Known range from Bering Sea, Alaska to southern Baja California (Haderlie and Abbott 1980).

Local Distribution: Oregon distribution along open coasts and in estuaries including

Yaquina (Betcher et al. 2012) and Coos Bays and the Charleston boat basin.

Habitat: Wood that is floating or in piles, but individuals do not burrow in buried wood (Haderlie and Abbott 1980). Great efforts have been made to discourage settlement and destruction of coastal man-made wooden structures. Some repellents slow, but do not completely deter the shipworm. (see also **Behavior**).

Salinity: Prefers full strength sea water (particularly for spawning, Kabat and O'Foighil 1987) of open oceans and doesn't tolerate reduced salinity (Ricketts and Calvin 1971). Can survive in salinities up to 50 (Haderlie and Abbott 1980).

Temperature: Prefers cold habitats and tends to lay eggs during the coldest months. Reported temperature range (Puget Sound, Washington) is from 7 to 12°C (Johnson and Miller 1935; Betcher et al. 2012).

Tidal Level: Subtidal to 70m. Individuals occur as deep as 200 meters (Monterey Bay, California, Haderlie 1983b), but are most dense at 0.3 meters above mudline (Haderlie and Mellor 1973). Individuals were also collected from wooden panels suspended at depths of 1–3 meters (Betcher et al. 2012).

Associates: Known macro invertebrate associates include small isopods from the genus *Limnoria* (e.g., see *Limnoria tripunctata*, this guide; Kozloff 1993) as well as the isopod *Ianiropsis derjugini* (see description in this guide), which was found in Charleston harbor with *B. setacea*.

Shipworms are also known to host a community of bacterial endosymbionts that aid in the digestion of consumed wood (Tryleik and Allen 1980; Siddall et al. 2009; Betcher et al. 2012). These symbionts are cellulolytic nitrogen-fixing bacteria and reside in the shipworm's gills (ctenidia) and are acquired by vertical transmission, i.e., from parent to offspring (Sipe et al. 200)

Abundance: As many as 720 per square meter at 60 meters deep, but fewer individuals in shallower water (Hill and Kofold 1927).

Life-History Information

Reproduction: Oviparous (Coe 1941). *Bankia setacea* exhibits protandric consecutive hermaphroditism, where all young begin as males and about half develop into females later in life (Coe 1941; Haderlie

and Abbott 1980; Kabat and O'Foighil 1987). Oocytes are 47–50 µm in diameter and sperm heads are 5 µm in length. Fertilization occurs outside burrows during coldest temperatures and in full strength salinity. Self-fertilization is possible (Coe 1941; Kabat and O'Foighil 1987). Spawning occurs year-round with peaks in Feb–May (Washington, Kabat and O'Foighil 1987) and fall and spring (southern California, Coe 1941) and can be triggered by a rapid change in water temperature or salinity (Quayle 1992). The complete development of *B. setacea* has not been described, but that of its Atlantic coast congener, *B. gouldi*, was described by Culliney in 1975.

Larva: Teredinidae developmental modes vary from brooding lecithotrophic larvae to planktotrophic larvae (Sipe et al. 2000). In *B. setacea*, development occurs in the lab at salinities from 16–40 and temperatures 8–14°C (Kabat and O'Foighil 1987). Following fertilization, free-swimming blastulae develop at 4–5 hours and embryos develop into trochophore larvae at 12–14 hours (Haderlie and Abbott 1980), which proceed to two shelled veliger larval stages, called prodissoconch I (the first and earliest shell, 120–130 µm) and II (200 µm) (Quayle 1992). Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e., snail-like versus clam-like). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger. In *B. setacea*, wild-caught larvae were described by Quayle (1953). Larval shell is almost round and becomes increasingly yellow with age and growth (e.g. prodissoconch II, for shell size and shape distribution, see Fig. 4, Brink 2001) at which point the shell has a distinct dark rim around the margin. *Bankia setacea* larvae have long pelagic life, and can swim up to four weeks in field conditions at 12–15°C (Quayle 1953) to two months in the lab at 15°C (Coe 1941; Kabat and O'Foighil 1987). Advanced larvae are 250 µm in length and resemble small bivalves and vertically migrate to the surface at night and six meters depths during the day (Kabat and O'Foighil 1987). They must settle on wood (Haderlie and Abbott 1980) and settlement occurs from

Oct–Dec (Puget Sound, Washington, Johnson and Miller 1935 in Coe 1941) or Oct–July (California). In the Port of Everett, Washington, settlement occurred year round and peaked from Aug–Oct, and may be prevented by high water temperatures in summer months. Settlement may be induced by waterborne cues from conspecifics or wood previously bearing conspecifics (Gara et al. 1997). Initial boring is done by the young larva, which creates a pin-sized hole that grows as the animal within it does (Ricketts and Calvin 1952).

Juvenile: Newly settled spat are 245 µm by 256 µm and develop pallets by the time they are 500–600 µm in length. They can completely cover themselves in a burrow within 24 hours of settlement and reach sexual maturity after as little as four months (Kabat and O’Foighil 1987). Males and females can be differentiated once they measure 20 to 50 cm (Coe 1941).

Longevity: Longest lived individuals were 8–14 months in one Monterey Bay, California study (Hill and Kofold 1927).

Growth Rate: Growth rate is temperature dependent with slowest growth occurring under 10°C (average 50 mm per month), fastest at over 10°C. (average 100 mm per month). The greatest individual growth observed was 610 mm in five months with burrow diameter of 12 mm (see Quayle in Haderlie and Mellor 1973). Research also suggests that growth rates depends on wood species and individual density (Quayle 1992).

Food: Wood (e.g. Douglas Fir, Fig. 3, Haderlie 1983a; Gara et al. 1997) as shipworms are able to digest cellulose. Although the nutritive quality of wooden material to the clam has been debated, it is likely that some wood is digested and nutrients absorbed by microvilli within a large caecum (see **Internal** body, Bazylinkski and Rosenburg 1983). *Bankia setacea* is also known to eat plankton (Haderlie and Abbott 1980) and filters water with ciliary action of ctenidia (Kozloff 1993).

Predators:

Behavior: Young *B. setacea* follow wood grain. Thus, burrows are parallel and do not intersect (Kozloff 1993). Several individuals (e.g., 1–10) can destroy untreated soft wood in less than a year (Walden et al. 1967; Haderlie and Abbott 1980). Boring rate is 2.7 cubic centimeters per month or about 49

cubic centimeters in a lifetime (Haderlie and Mellor 1973; Davidson and de Rivera 2012). *Bankia setacea* is a greater bioeroder than other burrowing and boring invertebrates (e.g., the burrowing isopod *Sphaeroma quoianum*, Davidson and de Rivera 2012). Individual “attacks” on wood are most common from July to February (see Fig. 22, Quayle 1992) and includes many local wood species (e.g., Alder, Birch, Maple, etc., Table 7, Quayle 1992).

Bibliography

1. BAZEYLINSKI, D. A., and F. A. ROSENBERG. 1983. Occurrence of a brush border in the caecum (Appendix) of several *Toredo* and *Bankia* species (Teredinidae: Bivalvia: Mollusca). *Veliger*. 25:251-254.
2. BETCHER, M. A., J. M. FUNG, A. W. HAN, R. O’CONNOR, R. SERONAY, G. P. CONCEPCION, D. L. DISTEL, and M. G. HAYGOOD. 2012. Microbial distribution and abundance in the digestive system of five shipworm species (Bivalvia: Teredinidae). *Plos One*. 7.
3. BORGES, L. M. S., H. SIVRIKAYA, A. LE ROUX, J. R. SHIPWAY, S. M. CRAGG, and F. O. COSTA. 2012. Investigating the taxonomy and systematics of marinewood borers (Bivalvia: Teredinidae) combining evidence from morphology, DNA barcodes and nuclear locus sequences. *Invertebrate Systematics*. 26:572-582.
4. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
5. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
6. COE, W. R. 1941. Sexual phases in wood-boring mollusks. *Biological Bulletin*. 81:168-176.
7. CULLINEY, J. L. 1975. Comparative larval development of shipworms

- Bankia gouldi* and *Teredo navalis*. Marine Biology. 29:245-251.
8. DAVIDSON, T. M., and C. E. DE RIVERA. 2012. Per capita effects and burrow morphology of a burrowing isopod (*Sphaeroma quoianum*) in different estuarine substrata. Journal of Crustacean Biology. 32:25-30.
 9. GARA, R. I., F. E. GREULICH, and K. L. RIPLEY. 1997. Shipworm (*Bankia setacea*) host selection habits at the Port of Everett, Washington. Estuaries. 20:441-449.
 10. HADERLIE, E. C. 1983a. Depth distribution and settlement times of the molluscan wood borers *Bankia setacea* (Tryon, 1863) and *Xylophaga washingtona* Bartsch, 1921, in Monterey Bay. Veliger. 25:339-&.
 11. —. 1983b. Long-term natural resistance of some central American hardwoods to attacks by the shipworm *Bankia setacea* (Tryon) and the gribble *Limnoria quadripunctata holthuis* in Monterey Harbor. Veliger. 25:182-&.
 12. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. In: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 13. HADERLIE, E. C., and J. C. MELLOR. 1973. Settlement, growth rates and depth preference of the shipworm *Bankia setacea* (Tryon) in Monterey Bay. Veliger. 15:265-286.
 14. HILL, C. L. R., and C. A. E. KOFOLD. 1927. Marine borers and their relation to marine construction on the Pacific coast, being the final report of the San Francisco Bay Marine Piling Committee. Calif., The Committee, San Francisco.
 15. JOHNSON, M. W., and R. C. MILLER. 1935. The seasonal settlement of shipworms, barnacles, and other wharf-pile organisms at Friday Harbor, Washington. University of Washington Publications in Oceanography. 2:1-18.
 16. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. In: Reproduction and development of marine invertebrates of the northern Pacific Coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 17. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 18. LUI, D., and P. M. TOWNSLEY. 1968. Glucose metabolism in the caecum of the marine borer *Bankia setacea*. Journal of the Fisheries Research Board of Canada. 25:853-862.
 19. LUI, D., and C. D. WALDEN. 1970. Enzymes of glucose metabolism in the caecum of the marine borer *Bankia setacea*. Journal of the Fisheries Research Board of Canada. 27:1141-1146.
 20. QUAYLE, D. B. 1953. Marine boring and fouling organisms. Washington University Press, Seattle, WA.
 21. —. 1992. Marine wood borers in British Columbia. Canadian Special Publication of Fisheries and Aquatic Sciences. 115:I-IV, 1-55.
 22. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
 23. —. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
 24. SIDDALL, M. E., F. M. FONTANELLA, S. C. WATSON, S. KVIST, and C. ERSEUS. 2009. Barcoding bamboozled by bacteria: convergence to metazoan mitochondrial primer targets by marine microbes. Systematic Biology. 58:445-451.
 25. SIPE, A. R., A. E. WILBUR, and S. C. CARY. 2000. Bacterial symbiont transmission in the wood-boring shipworm *Bankia setacea* (Bivalvia: Teredinidae). Applied and Environmental Microbiology. 66:1685-1691.
 26. TRYTEK, R. E., and W. V. ALLEN. 1980. Synthesis of essential amino acids by bacterial symbionts in the

gills of the shipworm *Bankia setacea* (Tryon). *Comparative Biochemistry and Physiology: A-Physiology*. 67:419-427.

27. TURNER, R. D. 1966. A survey and illustrated catalogue of the Teredinidae (Mollusca: Bivalvia). Museum of Comparative Zoology, Harvard, Cambridge, Massachusetts.
28. WALDEN, C. C., I. V. F. ALLEN, and P. C. TRUSSELL. 1967. Estimation of marine-borer attack on wooden surfaces. *Journal of the Fisheries Research Board of Canada*. 24:261-272.

Updated 2015

Adula californiensis

The pea pod borer

Phylum: Mollusca
Class: Bivalvia, Pteriomorpha
Order: Mytiloida
Family: Mytilidae

Taxonomy: This species was originally described under the name *Modiola californiensis* by Philippi in 1847, but was transferred to the genus *Adula* in 1857 by Adams and Adams. Additional, but uncommon, synonyms include *Adula styliina* (Huber 2010). Dall (1921) and Rocque (1953) have included *Adula* in the genus *Botula*, but Soot-Ryen (1955) differentiated the two genera. Ockelmann and Dinesen (2009) found these two genera to be distantly related, and suggested evidence for a well-defined genus *Adula* within the Mytilinae (Ockelmann and Dinesen 2009).

Description

Size: Individuals up to 40 mm in length and 10 mm in height.

Color: Shell exterior brown to black (Mytilidae, Coan and Valentich-Scott 2007), interior white, sub-nacreous, with posterior edge that is tinged with blue. Worn beaks, anteriorly, show white, and periostracum is thin, brown, and lacquer-like (Fig. 1). No chalky incrustations on shell (*Adula*, Coan and Valentich-Scott 2007).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Mytilids have cylindrical shells and two adductor muscles, with associated scars that are unequal in size (see Plate 395, Coan and Valentich-Scott 2007). Mytilids often use byssal threads to maintain contact with the substratum (Kozloff 1993).

Body: (see plate 17, Kozloff 1993)

Color:

Interior:

Exterior:

Byssus: Hairy threads which attach mussel to substrate, appear on *Adula* as a large hairy posterior patch encrusted with mud and debris (Fig. 1).

Gills:

Shell: (see Plate 403C, Coan and Valentich-Scott 2007) Valves are deep and subequal,

cylindrical, do not taper, and are thin and fragile. Dorsal and ventral margins are parallel for at least half of their length (Keep and Longstreth 1935). Umbones extend one quarter of the way from anterior end (i.e. subterminal), are not prominent, and extend higher than posterior end (Packard 1918). Shell elongate and tapers posteriorly. The posterior and anterior ends are of equal thickness (Coan and Valentich-Scott 2007).

Interior: Muscle scars very unequal in size (Mytilidae, Coan and Valentich-Scott 2007), although faint crenulations appear on the dorsal anterior margin (Fig. 2). Hinge is about one quarter of the way from anterior end.

Exterior: Surface with some radial sculpture, particularly at the anterior end, but no patches of vertical file-like striations (Fig. 1). Shells are often eroded near the beaks, anteriorly (Haderlie and Abbott 1980).

Hinge:

Eyes:

Foot:

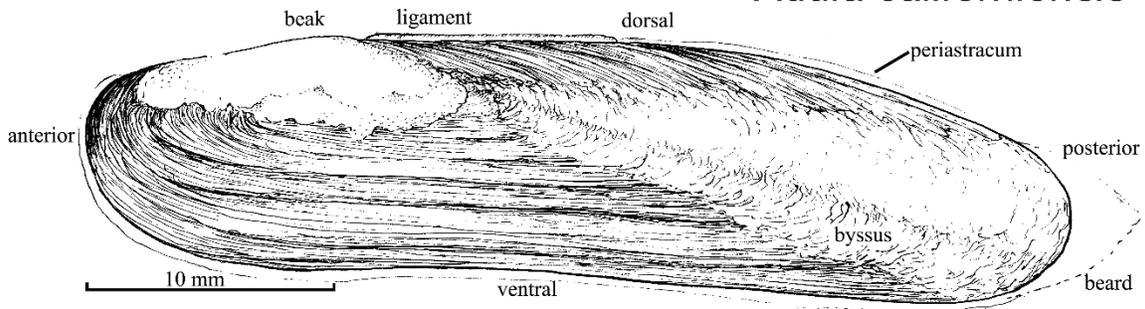
Siphons: White and fused almost to end. The incurrent siphon is with feathery oak leaf-shaped tentacles, in the illustrated specimen (Fig. 4).

Burrow:

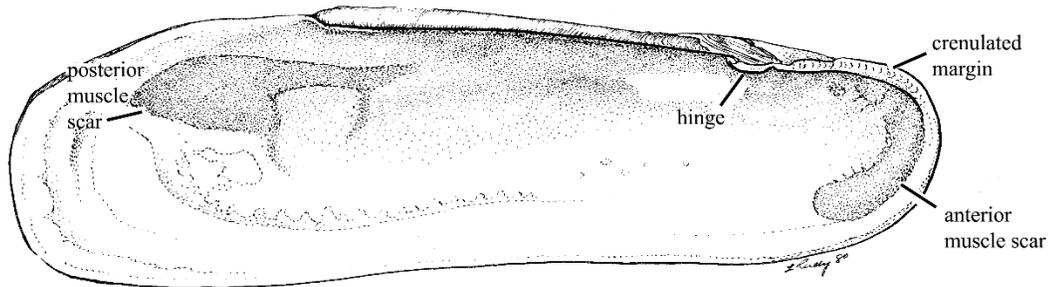
Possible Misidentifications

The family Mytilidae is characterized by two adductor muscles and associated scars that are unequal in size; the anterior scars are smaller and near the shell beak (see Plate 395, Coan and Valentich-Scott 2007). Members of this family have cylindrical shells that are dark brown or black that sometimes taper anteriorly, and the two shell valves are of similar morphology. They lack both a chondrophore (e.g., compare to *Mya arenaria*, this guide) and dorsal margin ears, and the shell is not cemented to the substratum (Coan and Valentich-Scott 2007). There are nearly 20 local species in the family Mytilidae comprising the genera *Septifer* (*S. bifurcatus*), *Lithophaga* (*L. plumula*), *Geukensia* (*G. demissa*), *Musculista* (*M. senhousia*),

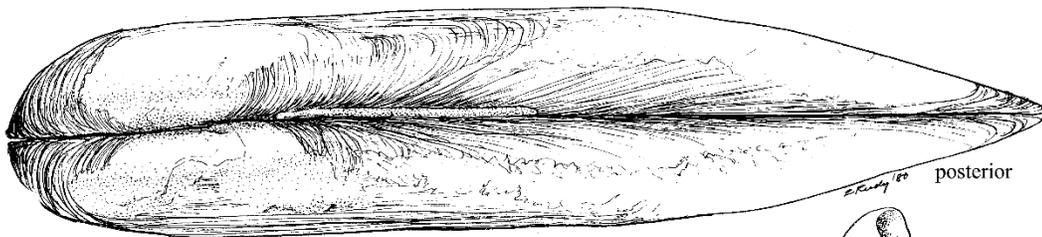
Adula californiensis



1. *Adula californiensis* x4.5: cylindrical shells, valves subequal; dorsal and ventral margins roughly parallel; smooth periostracum; posterior slope hairy; worn beaks 1/4 of way from rounded anterior; ligament external; radial sculpture.

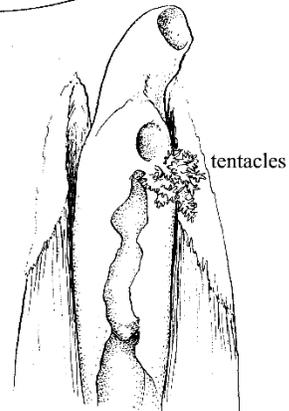


2. Left valve, interior: posterior muscle scar much larger than anterior scar; color white; sub-nacreous, posterior tinged with blue; anterior margin slightly crenulate; hinge without teeth.



3. (Dorsal view): posterior pointed; beaks not prominent.

4. Siphons:
white, fused almost to ends;
incurrent siphon with oak-leaf
like tentacles.



Modiolus (six species) and *Mytilus* (one to four species). Other genera are possibly present in the area, but are not included in current keys including *Crenella* (*C. decussata*), *Gregariella* (*G. coarctata*), *Solamen* (*S. columbianum*) (Coan and Valentich-Scott 2007).

Genera included in the current key can be differentiated as follows: *Mytilus* species (see *M. trossulus*, this guide) have shells that with beaks at the terminal portion of the anterior end and lack internal septa, while *Septifer* species possess an internal septum at their anterior end. All other genera have shells with beaks that are anterior, but not terminal. Of those, *Lithophaga plumula* individuals are with cylindrical shells and a posterodorsal slope that is rough and with chalky encrustations, while *Adula* species have a posterodorsal slope without chalky encrustations and, instead, have a thick mat and are sometimes covered with mud or debris. The genera *Geukensia*, *Modiolus*, and *Musculista* have shells that are not cylindrical, *G. demissa* shells have prominent ribs externally and are dark brown or black in color. *Modiolus* and *Musculista* species have shells without external ribbing and members of the former genus have periostracial hairs while *Musculista* do not.

The genus closest to *Adula* is *Lithophaga* (the “date shell”), a boring mussel with cylindrical shell and roughly parallel margins. It lacks the hairy posterior of *Adula*, and bores in hard rock and it has peculiar feather-like wrinkling on the posterior of the shell. There are three local species of *Adula* including *A. gruneri*, *A. diegensis*, and *A. californiensis*. *Adula gruneri* (= *A. falcata*, *Lithodomus falcatus*, Ockelmann and Dinesen 2009) and *A. californiensis* both bore into shale, while *A. diegensis* is free-living. *Adula gruneri* can be recognized from the other two by the presence of periostracum that is with irregular striae. *Adula californiensis* and *A. diegensis* can also be differentiated as the former species has an elongate shell, while *A. diegensis* has a stout shell. *Adula diegensis* also has a dorsal margin that flares and sparse periostracal mat on the posterior slope, neither are present in *A. californiensis*. *Adula diegensis* is a small species (< 19 mm in length) that occurs as

far north as San Francisco, California, on mudflats and pilings with other mussels (e.g., see *Mytilus trossulus*, this guide). It is polished and dark blue interiorly. *Adula gruneri*, the hooked pea-pod shell, bores deep into hard rock as well as into clay. It has wrinkled periostracum, not a smooth one, as well as vertical striae to assist in boring. Its shell is more angular and proportionally longer than the more cylindrical than *A. californiensis*, and tapers posteriorly. The beaks in *A. gruneri* are situated at about the anterior eighth of the shell length, and are strongly involute (closely wound). Its northern limit is probably Coos Bay and is known from southern Oregon to Baja California, as is *A. diegensis* (Kozloff 1993). *Adula gruneri* is the largest of the three *Adula* species, at up to 80 mm in length, while *A. diegensis* is generally smaller (~20 mm) than *A. californiensis* (Kozloff 1993). (For in depth differentiation between *Adula* species, see Ockelmann and Dinesen 2009.)

Ecological Information

Range: Type region in northwestern Pacific (Bernard 1983). Known range includes Vancouver Island, British Columbia, Canada, Alaska, and San Diego, California (Kozloff 1993).

Local distribution: Local distribution at sites in Coos Bay and Pigeon Point, also Yaquina and Boiler Bays (see Fig. 1, Lough and Gonor 1971).

Habitat: Burrows into soft, muddy shale or is, occasionally, free-living (Coan and Valentich-Scott 2007). In Coos Bay, they can be found in in old pholad (fam. Pholadidae) burrows.

Distribution is limited by appropriate burrowing substrate (Lough and Gonor 1971).

Salinity: Collected at salinities of 30, usually in the lower reaches of the bay where salinity is relatively high and constant. Estuarine and marine habitats (Lough and Gonor 1971).

Temperature: Individuals occur in temperate waters.

Tidal Level: Intertidal to sublittoral (Coan and Valentich-Scott 2007). Individuals collected from up to 10 meter depths (Newport, OR, Lough and Gonor 1971).

Associates: Associates include the terebellid polychaete *Thelepus*, the pholad *Penitella*, and the brachyuran crab, *Cancer oregonensis*. In addition, *A. californiensis*

hosts several ciliated protozoans including *Raabella* (= *Hypocomides*) *botulae*, *R. parva* and *Insignicoma venusta* (Coan and Valentich-Scott 2007).

Abundance: not common

Life-History Information

Reproduction: Dioecious, and free-spawning. Individuals are ripe from June to October (Oregon, Kozloff 1974; Lough and Gonor 1971). Oocytes are 70–80 µm in diameter and are pink to orange in color and yolky (Lough and Gonor 1971). For sperm morphology of members of the Mytilidae, including the conger, *A. falcatoides*, see Kafanov and Drozdov 1998.

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e., snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the “D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone. Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig. 1, Kabat and O’Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001). Development in *A. californiensis* was described by Lough and Gonor (see Fig. 2, 1971) and proceeds with polar lobe formation within the first hour, which is resorbed by 1.5 hours, first and second cleavages at 1.5 and 2.5 hours post fertilization, respectively, trochophore larvae develop at 15 hours, the shell gland forms at at 31 hours, and a bivalve shell, that surrounds individuals entirely, is complete at 72 hours (at 15°C, Lough and Gonor 1971). Veliger larvae are free-swimming (Brink 2001) and are relatively tolerant of low salinity but not high temperatures (Kabat and O’Foighil 1987). While trochophore larvae tend to swim in all directions, veligers swim vertically and not

horizontally (Lough and Gonor 1971; Haderlie and Abbott 1980). Settlement and metamorphosis occur after three days. Larval size is approximately 108 µm at 3 days, 117 µm at 15 days and 119 µm at 25 days post fertilization (Lough and Gonor 1971).

Development increases with temperature and slows with decreasing salinity, with lowest salinity for development 26.3 (Lough and Gonor 1971). Young larvae (3 days old) are more sensitive to a reduction in salinity than older larvae (15 days old or more), but the opposite trend is seen for temperature tolerance (older larvae have a narrower temperature tolerance) (Lough and Gonor 1973a, b). Ideal temperature and salinity for development is 10–15°C and salinity 31–33 (Lough and Gonor 1973a).

Juvenile: Juveniles morphology flares posteriorly rather than being cylindrical (i.e. modioliform).

Longevity:

Growth Rate:

Food: A suspension feeder. For feeding mechanisms and concentration of particles using currents produced by cilia in the congener, *A. gruneri*, see Fankboner 1971.

Predators:

Behavior: This species is probably more of a nestler than a burrower.

Bibliography

1. BERNARD, F. R. 1983. Catalogue of the living bivalvia of the eastern Pacific Ocean : Bering Strait to Cape Horn. Ottawa : Dept. of Fisheries and Oceans, Ottawa.
2. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
3. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In*: The Light and Smith manual: intertidal invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
4. DALL, W. H. 1921. Summary of the marine shellbearing mollusks of the northwest coast of America, from San Diego, California to the Polar Sea.

- Bulletin of the United States Natural Museum. 112:1-217.
5. FANKBONER, P. V. 1971. Ciliary currents associated with feeding, digestion, and sediment removal in *Adula* (*Botula*) *falcata* Gould 1851. Biological Bulletin. 140:28-45.
 6. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 7. HUBER, M. 2010. Compendium of bivalves: a full-color guide to 3,300 of the world's marine bivalves. A status of bivalvia after 250 years of research. Conch Books, Hackenheim.
 8. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the Northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 9. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
 10. KEEP, J., and J. LONGSTRETH. 1935. West coast shells: a description in familiar terms of the principal marine, fresh-water, and land mollusks of the United States, British Columbia, and Alaska, found west of the Sierra. Stanford University Press, Stanford, CA.
 11. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
 12. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 13. LA ROCQUE, A. L. 1953. Catalogue of the recent Mollusca of Canada. E. Cloutier, Queen's Printer, Ottawa.
 14. LOUGH, R. G., and J. J. GONOR. 1971. Early embryonic stages of *Adula californiensis* and the effect of temperature and salinity on developmental rate. Marine Biology. 8:118-125.
 15. —. 1973a. A response-surface approach to the combined effects of temperature and salinity on the larval development of *Adula californiensis* (pelecypoda:mytilidae) I. survival and growth of three and fifteen-day old larvae. Marine Biology. 22:241-250.
 16. —. 1973b. A response-surface approach to the combined effects of temperature and salinity on the larval development of *Adula californiensis* (Pelecypoda:Mytilidae) II. long-term larval survival and growth. 22:295-305.
 17. OCKELMANN, K. W., and G. E. DINESEN. 2009. Systematic relationship of the genus *Adula* and its descent from a *Mytilus*-like ancestor (Bivalvia, Mytilidae, Mytilinae). Steenstrupia. 30:141-152.
 18. PACKARD, E. L. 1918. Molluscan fauna from San Francisco Bay. Zoology. 14:199-452.
 19. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides: an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford, Stanford University Press, Stanford.
 20. —. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
 21. SOOT-RYEN, J. 1955. A report on the family Mytilidae (Pelecypoda). Allan Hancock Pacific Expedition. 20:1-174.
 22. WILSON, B. R. 2006. A new generic name for a burrowing mytilid (Mollusca: Bivalvia: Mytilidae). Molluscan Research. 26:89-97.

Updated 2016

Mytilus trossulus

The bay mussel

Phylum: Mollusca
Class: Bivalvia, Pteriomorpha
Order: Mytiloidea
Family: Mytilidae

Taxonomy: Confusion has surrounded the taxonomy of *Mytilus* species because the genus has historically been based on morphological shell characters, which have been shown to be plastic and varies with habitat (e.g. see **Growth**, Gosling 1992a and b). *Mytilus trossulus* is the species native to the west coast of North America, and was previously confused with *M. edulis*. Thus, in many intertidal guides of the past, (e.g., Kozloff 1993; Ricketts and Calvin 1952; Kabat and O'Foighil 1987; Haderlie and Abbott 1980) *M. edulis* is actually *M. trossulus*. Many of the references to which we refer are for *M. edulis* (and we call *M. trossulus*, for clarity). *Mytilus trossulus* is a member of the *Mytilus edulis* species complex, a group of three sibling species (*M. trossulus*, *M. edulis*, *M. galloprovincialis*), recently differentiated using molecular methods (McDonald and Koehn 1988; Gosling 1992a and b; Seed 1992; Geller 2007). The three species can be defined by both molecular and, less easily by, morphological characters (McDonald et al. 1991) (see **Range**). Additional north Pacific and Arctic synonyms for *M. trossulus* include (but are not limited to): *M. glumeratus*, *M. pedroanus*, *M. edulis latissimus*, *M. edulis kussakini*, *M. edulis declinis*, *M. septentrionalis*, *M. ficus*, McDonald and Koehn 1988; Kafanov 1999).

Description

Size: Individual size is about 70–110 mm (Coe 1945; Kozloff 1974; Haderlie and Abbott 1980). Mean dry body weight is 7 grams (Harger 1968).

Color: Blue, violet and white shell with shiny brown-black periostracum. Blue-black color particularly around ventral (posterior) shell margin. Tissues are orangish-tan.

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Mytilids have roughly cylindrical shells and two adductor muscles, with associated

scars that are unequal in size (see Plate 395, Coan and Valentich-Scott 2007). Mytilids often use byssal threads to connect them to the substratum (Kozloff 1993).

Body:

Color:

Interior: *Mytilus trossulus* as well as other bivalves can develop hemic neoplasia, a blood cell disorder that is often linked to environmental contaminants (e.g. polycyclic aromatic hydrocarbons, chlorinated hydrocarbons). Up to 30% of *M. trossulus* in Puget Sound, WA were infected. (Krishnakumar et al. 1999). A widely prevalent genus, the physiology of *Mytilus* has been the subject of much research (e.g., Smith 1982).

Exterior:

Byssus:

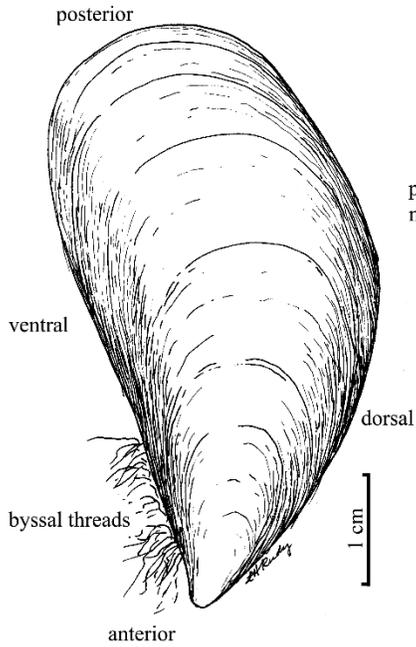
Gills:

Shell: Pointed shell, anteriorly, with very broad posterior (Haderlie and Abbott 1980). Individuals that are exposed to more wave action have shells that are thicker and grow more slowly (Haderlie and Abbott 1980).

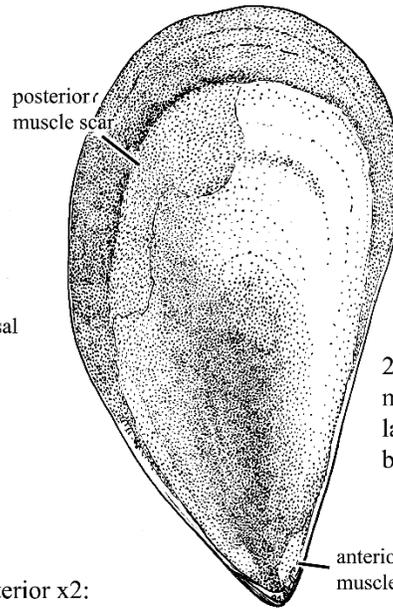
Interior: Large posterior muscle scar, small anterior scar that is near the beak on the anterior ventral margin (Fig. 2). Pit-like byssal gland is present at the base of foot and produces liquid that hardens into byssal threads which are visible on the ventral shell margin (Fig. 1). Digestion is both intra and extra cellular, and is aided by the crystalline style and associated enzymes (Haderlie and Abbott 1980).

Exterior: Valves of similar morphology, wedge-shaped, and longer than high. Shell regular, smooth, and with concentric growth lines, but no radial ribs (Fig. 1, compare to *Clinocardium nuttallii*, this guide). Fine byssal threads attach to substrate, and beaks (the most prominent point on the shell, or umbo) are anterior and terminal. The shell is made of calcium, which is absorbed from the surrounding seawater, and precipitated at the shell edge under the periostracum (Haderlie and Abbott 1980).

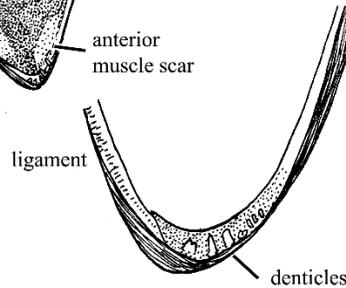
Mytilus trossulus



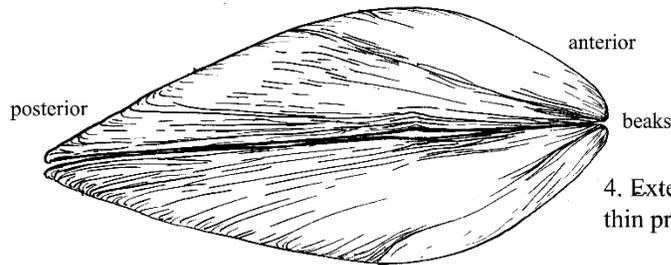
1. *Mytilus trossulus*, right valve, exterior x2: smooth, tapering, like valves; concentric lines only; beaks terminal.



2. Interior, right valve: muscle scars unequal: posterior large, anterior small, near beak; blue-black around margin.



3. Hinge area: no teeth, only small denticles; no shell-like septum.



4. Exterior (lateral, ventral view): thin profile; terminal beaks.

Hinge: No hinge teeth or chondrophore but small denticles are present near the beak. No shell-like septum (or shelf) at anterior end (Fig. 4).

Eyes:

Foot: Foot is reduced and internal. Although individuals are attached to substrate by byssal threads, they are capable of moving. By extending the foot and attaching it to the substrate, they are able to break byssal threads a few at a time and, eventually, detach and move to another location where they use their foot to reattach (Ricketts and Calvin 1952).

Siphons: No siphons, instead there are undulating openings between mantle edges (especially conspicuous along the posterior margin).

Burrow:

Possible Misidentifications

The family Mytilidae is characterized by two adductor muscles and associated scars that are unequal in size; the anterior scars are smaller and near the shell beak (see Plate 395, Coan and Valentich-Scott 2007). Members of this family have cylindrical shells that are dark brown or black that sometimes taper anteriorly, and the two shell valves are of similar morphology. They lack both a chondrophore (e.g., compare to *Mya arenaria*, this guide) and dorsal margin ears, and the shell is not cemented to the substratum (Coan and Valentich-Scott 2007). There are nearly 20 local species in the family Mytilidae comprising the genera *Septifer* (*S. bifurcatus*), *Lithophaga* (*L. plumula*), *Geukensia* (*G. demissa*), *Musculista* (*M. senhousia*), *Modiolus* (six species) and *Mytilus* (one to four species). Other genera possibly present in the area, but not included in current keys, may include *Crenella* (*C. decussata*), *Gregariella* (*G. coarctata*), and *Solamen* (*S. columbianum*) (Coan and Valentich-Scott 2007).

Genera can be differentiated as follows: *Mytilus* is a cosmopolitan genus with at least four species (Koehn 1991), has shells with beaks at the terminal portion of the anterior end and lack internal septa, while *Septifer* species possess an internal septum at their anterior end. All other genera have shells with beaks that are anterior, but not terminal. Of those, *Lithophaga plumula* individuals are with cylindrical shells and a

posterodorsal slope that is rough and with chalky encrustations, while *Adula* species have a posterodorsal slope without chalky encrustations and, instead, have a thick mat and are sometimes covered with mud or debris. The genera *Geukensia*, *Modiolus*, and *Musculista* have shells that are not cylindrical, *G. demissa* shells have prominent ribs externally and are dark brown or black in color. *Modiolus* and *Musculista* species have shells without external ribbing and members of the former genus have periostracial hairs while *Musculista* do not.

Species in the genus *Mytilus* are difficult to differentiate morphologically. The three local species are *M. californianus*, *M. trossulus*, and *M. galloprovincialis* (Evans et al. 2010). *Mytilus californianus* has a shell with radial ribs that are conspicuous, especially near the shell posterior. On the other hand, *M. trossulus*, *M. galloprovincialis* and *M. edulis* all have smooth shells and are lumped into the *M. edulis* species complex. Recent genetic research has shown that the smooth species that is present locally is *M. trossulus*. However, this species overlaps and forms a hybrid with *M. galloprovincialis* to the south in central California. The latter species has also been observed in BC Canada, but their current range includes only central California south to Baja California. Of these three species, only *M. trossulus* is native to the north Pacific, while *M. galloprovincialis* is native to Europe and *M. edulis* to the north Atlantic. *Mytilus trossulus* is often found with *Mytilus californianus*, the larger, coarser "common mussel" of the West Coast. Internally *M. californianus* is orange, but the most dependable distinguishing characteristic is the presence of radial ridges in *M. californianus*. When small, the two are more difficult to distinguish, however, *M. trossulus* has sharper edges, a thinner profile (Fig. 3), finer byssal threads, and more delicate concentric rings than does *M. californianus*. It also can be found higher in the intertidal zone, in more protected spots, not on exposed rocks with heavy surf and turbulence. In profile, *M. galloprovincialis* shells are higher and flatter than *M. trossulus* and the anterior end is beaked in the former species, while it is blunt in the latter. Adductor muscles scars are also different between the two species. The anterior scars are small and round in *M. galloprovincialis*

and narrow to elongate in *M. trossulus* (see Fig. 1.2 Gosling 1992b). *Mytilus trossulus* is more elongate than *M. edulis*, with which it co-occurs in eastern Newfoundland (Innes and Bates 1999). Few, if any, morphological characters (e.g., shell shape) can be used to reliably differentiate *M. edulis* and *M. trossulus* (McDonald et al. 1991; Seed 1992; Sarver and Foltz 1993). Fortunately, they do not co-occur in Oregon, as they do in the north Atlantic (Varvio et al. 1988; Mallet and Carver 1995; Kafanov 1999; Liu et al. 2011), where less hybridization has been observed between sympatric populations (Toro et al. 2002; Vainola and Strelkov 2011; Tam and Scrosati 2014). Larval characters were proposed for higher-level classification in the Mytilinae by Evseev et al. (2011).

Other rarer mussels include *Modiolus* sp., the horse mussel, which has external subterminal beaks and is brown and hairy. This species is found in clumps in the mud subtidally. *Septifer bifurcatus* is found under rocks, is black outside, purple within, and with definite radiating ribs and shell-like septum across the anterior end.

Ecological Information

Range: *Mytilus trossulus* was originally described from Tillamook, OR and Puget Sound, Washington (= "Killimook and Puget Sound, Oregon" McDonald and Koehn 1988; Kafanov 1999), but due to recent understanding of the *M. edulis* species complex, a neotype designation was suggested from molecularly identified shells by Kafanov (1999). *Mytilus trossulus* is the native smooth blue mussel from the northeast Pacific and ranges from the Arctic to central California. Also in Hokkaido in the northwest Pacific (Suchanek et al. 1997). Although *Mytilus edulis* was previously believed to be the predominant species in northern Europe, *M. trossulus* is also widespread there (Vainola and Strelkov 2011). The congeneric species, *M. galloprovincialis* (the only *Mytilus* species to invade new regions, Braby and Somero 2006), is native to Europe but was introduced to the west coast of North America and now has a distribution that overlaps with *M. trossulus* in central California, and extends south to Baja, California. Where the two species meet, between Monterey and Cape Mendocino, they form a hybrid zone (Braby and Somero 2006). Additional hybrid zones

noted between the two species include Whidbey Island, Washington, San Francisco and San Diego Bay, California (Suchanek et al. 1997). The final member of this species complex, *M. edulis*, is native to the north Atlantic (Coan and Valentich-Scott 2007). *Mytilus trossulus* was previously mistaken for *M. edulis* before molecular work (McDonald and Koehn 1988; Varvio et al. 1988; McDonald et al. 1991; Vainola and Hvilson 1991; Seed 1992; Sarver and Foltz 1993; Geller et al. 1994; Beynon and Skibinski 1996; Burzynski et al. 2003; Wood et al. 2003) revealed the native local species was *M. trossulus* (see **Taxonomy**). Previous descriptions of *M. edulis* include a range from the Bering Sea, Alaska to Mexico (Ricketts and Calvin 1952), but the current distribution of *M. edulis* includes the north Atlantic (where it co-occurs with *M. trossulus*) and in the temperate southern Hemisphere (e.g., Chile). This species complex, including the three species discussed, has been the subject of considerable population genetic research (e.g., Koehn 1991; Riginos and Cunningham 2005), particularly work on hybridization and mitochondrial introgression (from *M. trossulus* into *M. galloprovincialis*, Geller et al. 1994; Geller 1994; Rawson and Hillbish 1995; Rawson et al. 1996).

Local Distribution: Likely occurs in all Oregon estuaries as well as along the outer coast (with the congener, *M. californianus*).
Habitat: *Mytilus trossulus* is an extremely adaptable species. Individuals will attach to rock, wood, fiberglass, and firm mud. They prefer pilings in polluted harbors (Ricketts and Calvin 1971) and quiet waters. The congener, *M. californianus*, is more common on open coasts in the rocky intertidal and is well known for its interaction with the sea star, *Pisaster ochraceus* (see description in this guide) and the resulting intertidal vertical zonation; the upper limit is determined by physiological stress of aerial exposure and the lower limit is set by predation from the sea star (Niesen 2007). *Mytilus galloprovincialis* and *M. trossulus* occur in rocky intertidal habitats, but are limited by stresses (e.g. temperature and predation) that do not affect the thicker-shelled species, *M. californianus*, as greatly (Evans and Somero 2010). Meanwhile, *M. californianus* is competitively excluded by the congeners in bay and estuarine habitats because of a lower

tolerance to variable osmotic gradients (Evans and Somero 2010). *Mytilus* species, including *M. trossulus*, are indicators of ecosystem health (e.g., lead, Haderlie and Abbott 1980; polycyclic aromatic compounds, Hellou and Law 2003; Turja et al. 2013; Turja et al. 2014; Preece et al. 2015).

Salinity: *Mytilus trossulus* is better adapted to variable (particularly lower) salinity than other *Mytilus* species, particularly larval stages, which may facilitate the current geographic distribution of species (see **Range**) (e.g., *M. edulis*, *M. galloprovincialis*, Sarver and Foltz 1993; Qui et al. 2002; Evans and Somero 2010, but see also Gardner and Thompson 2001; Kotta et al. 2015). *Mytilus edulis* can tolerate lower salinity than can *M. californianus* (Kozloff 1993). Adults prefer salinities of 2–33, need periods of desiccation and require less oxygenation than does *M. californianus*. Larvae of *M. edulis* can't survive at salinities over 45 or under 10 (Field 1922; Qui et al. 2002).

Temperature: Mussels potentially experience maximal thermal stress in intertidal zones due to long periods of aerial exposure and black shells (Hofman and Somero 1995; Tomanek and Zuzow 2010). *Mytilus trossulus* is a temperate and cold-water species; it becomes more abundant in the northern reaches of its range (Ricketts and Calvin 1971), where it encounters optimum growth temperature of 10–20°C (Haderlie and Abbott 1980). *Mytilus galloprovincialis*, on the other hand, is warm-adapted due to its native habitat in the Mediterranean Sea (Evans and Somero 2010) and temperature limitation largely contributes to the distribution of these species on the west coast of North America. In fact, Geller et al. (1994) found that *M. galloprovincialis* was not able to establish itself in northern regions despite the fact that their larvae were being transported in ballast water from Japan.

Tidal Level: Generally found from mean low to mean higher low, but can occur from -0.3 to +1.5 meters. Subtidal distribution reported to 40 m in bays and sheltered areas (Haderlie and Abbott 1980; e.g., on pilings, Kotta et al. 2015). Also found around (both higher and lower in the intertidal) clumps of *M. californianus* (Ricketts and Calvin 1971; Akester and Martel 2000).

Associates: *Mytilus trossulus* can be the dominant member of a diverse community of invertebrates that include the barnacle, *Balanus glandula* (on mussel shells), nematodes, polychaetes (e.g., sabellid, serpulid, nereid, syllid), nemerteans, flatworms, the limpet *Lottia*, the bryozoan *Bugula*, anemone *Metridium senile*, the gastropod *Nucella*, red algae, tunicates, and hydrozoans (e.g. *Phialella fragilis*) (Haderlie and Abbott 1980; Niesen 2007; Mills et al. 2007). Some *Mytilus trossulus* are found in all *M. californianus* beds, which constitute a well-studied community (Ricketts and Calvin 1971). A blackish little sea cucumber, *Cucumaria pseudocurata*, is also found in mussel beds (e.g., especially *M. californianus*) (Kozloff 1993). Often occurs in clumps with *Septifer bifurcatus* nestled in and near the substrate (Haderlie and Abbott 1980). Parasites which can be present in *M. trossulus* include the copepod *Modiolicola gracilis* (gills), and *Mytilicola orientalis* (rectum) (Haderlie and Abbott 1980). *Mytilus* species also host pyramidellid and eulimid snails (Kuris 2007) and *M. trossulus*, specifically, hosts several ciliated protozoans (e.g. *Ancistrum mytili*, *A. caudatum*, *Crebricoma carinata*, *Raabella helensis*, Landers 2007) as well as the orthonectid, *Stoechothrum fosterae* (Kozloff 2007). *Mytilus* species also host commensal pea crabs *Fabia subquadrata* and *Opisthopus transversus* (Haderlie and Abbott 1980). *Mytilus trossulus* competes with macrophytes for space in the rocky intertidal (Kotta et al. 2015).

Abundance: Most abundant in northern portion of distribution (e.g. Oregon and Washington, Ricketts and Calvin 1971; Suchanek et al. 1997). A community can re-establish in three years and is subject to greater fluctuations in numbers than is *M. californianus* (Ricketts and Calvin 1971). Density of *M. trossulus* correlates with habitat, as individuals in very sheltered habitats are large and in low densities where the opposite is true for less sheltered habitats (Tam and Scrosati 2014). Abundance of *Mytilus* spp. larvae, including *M. trossulus*, ranged from over 1,000 to less than 1 individual per cubic meter (Coos Bay, OR, Shanks and Shearmann 2009, 2011) and larval abundances of 2500–4000 individuals per

cubic meter have been reported for *M. edulis* (Bay of Fundy and Oslofjord, Bayne 1976).

Life-History Information

Reproduction: Dioecious and free spawning (Field 1922), but hermaphroditism has been observed. Spawning occurs in late fall and winter in central California and November through May in southern California (MacGinitie and MacGinitie 1949; Haderlie and Abbott 1980). Individuals spawn in fall and winter on outer coasts and April–May in Puget Sound, BC, Canada and the San Juan Archipelago. Spawning duration in *M. trossulus* in the north Atlantic was longer than for *M. edulis*, which spawned for a period of 2–3 weeks in July (Toro et al. 2002). *Mytilus californianus*, on the other hand, spawns year round in southern California (mostly from Oct–March) and April to May in the San Juan Archipelago (Kabat and O’Foighil 1987). Oocytes are about the same size as *M. trossulus* at 60 µm and orange in color. Sperm morphology was described by Kafanov and Drozdov (1998); the sperm nucleus is 2 µm in length, the acrosome 2–5 µm and the sperm head is flask shaped in *Mytilus* species (see Fig. 2, Kafanov and Drozdov 1998). All three *Mytilus* species exhibit doubly uniparental mitochondrial inheritance, as females inherit mtDNA from their mother only, while males inherit both from mother and father (Rawson and Hillbish 1995; Zbawicka et al. 2007, 2010).

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning, through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the “D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone. Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig.

1, Kabat and O’Foighil 1987; Fig. 1, for a generalized life cycle, Brink 2001). For a full description of development in the laboratory see *M. edulis* in Kabat and O’Foighil 1987 (and references therein). Oocytes are 60–65 µm in diameter and surrounded by a thin egg envelope, but no jelly. Development proceeds as follows: 1st polar bodies form at 1 hour post-fertilization, embryos are ciliated and swimming at 6 hours, trochophore larvae at 24 hours, velar lobes and bivalved shell develops at 48 hours, larvae are straight hinge veligers at 42 hours, are at prodissoconch II at 66 hours post fertilization and have a foot (i.e. pediveligers) at 72 hours, (Kabat and O’Foighil 1987). Larvae have a relatively long pelagic duration of four weeks, thus this species has the potential to colonization a wide area and move great distances (Harger 1968). The straight hinge veliger larval stage occurs later in this species than in others, once individuals are 220 µm. At this time the umbo becomes rounded and the anterior lengthens, eventually sloping to a point (see Table 4, Brink 2001). Larval and juvenile morphology for *M. trossulus* were described by Evseev et al. in 2011 (see Fig. 2, Table 1). Larvae that are 270–290 µm have an ovate shell with symmetrical umbo, pointed anterior and rounded posterior. The hinge plate of the provinculum is 5–8 µm in height and includes 8–9 anterior, 15–17 central, and 7–8 posterior teeth and a lens-shaped pit ligament. Early juvenile shells are 360–380 µm and the umbo height is greater, anterior margin is broader, and posteroventral margin height increases; the conspicuous central teeth are 10–12 µm in height. Once 400–500 µm, shells are broad and enlarged posteroventrally, the umbo has low shoulders and is subtriangular, the hinge plate height continues to increase and the posterior teeth decrease in number to 5–7. The ligament pit becomes trapezoidal in shape, a lateral tooth develops at each anterior posterior margin, and an external ligament begins to form. At 600–700 µm juvenile teeth appear reduced, there are three teeth at the anterior and posterior margins, and the external ligament is 120–150 µm in length (Evseev et al. 2011). The larvae of *M. californianus* and *M. trossulus* are similar, but can be differentiated by the larvae of the former species having a less conspicuous, flatter umbo, and wider separation between the provincular lateral

teeth (Martel et al. 1999; see Fig. 5, Brink 2001). Larvae settle in summer in southern California, late spring, early summer in Puget Sound, Washington, and in summer on the east coast (Haderlie and Abbott 1980). Some secondary settlement occurs as individuals drift on their byssal threads (Kabat and O'Foighil 1987; Soo and Todd 2014), which allows for dispersal on weak currents (Haderlie and Abbott 1980). This so-called thread drifting has been observed in *Mytilus* spp., including *M. trossulus*, offshore of Coos Bay, OR (Shanks and Shearman 2011).

Mytilus californianus larvae are known to settle onto the byssal threads of conspecifics. Post-larval (> 5 mm) settlement in *M. trossulus* larvae was shown to be related to macroalgal and barnacle cover, water flux, tidal height and flushing time, and reflect the distribution and abundance of adults (Hunt and Scheibling 1996). The upper thermal and desiccation tolerances of larvae 1–2 mm was 34°C and at vapor pressure deficit levels of 1.01 kPa, respectively. The latter factor was more likely to be experienced by mussels at this study site (Barkely Sound, BC, Canada). It has been suggested that larvae settle within filamentous algae then relocate to adult habitats when 2–3 mm, a size at which individuals were more tolerant to desiccation (Jenewein and Gosselin 2013).

Juvenile: Juvenile size approximately 9–35 mm in length (Akester and Martel 2000), although 'early juvenile' may be as small as 360 µm (see Evseev et al. 2011, above). The posterodorsal margin becomes angular when shells are 900–1100 µm and at 1500–1700µm the shell is triangular and elongated ventrally, the ligament pit and juvenile teeth are covered by new shell growth and there are four lateral teeth at anterior and posterior margins (Evseev et al. 2011). Differentiating early juveniles in the genus *Mytilus* is challenging and Martel et al. 1999 proposed morphological characters to differentiate *M. californianus* from the bay mussels (*M. trossulus* and *M. galloprovincialis*): *M. californianus* juveniles have a more posterodorsal apex and a posterior muscle attachment that is larger (for additional characters, see Martel et al. 1999).

Longevity: Often the longest lived species in a community (e.g. southern California, Reish and Ayers 1968). Individuals that were 40–50

mm in length were 7–8 years old (Tam and Scrosati 2014).

Growth Rate: Individuals grow fastest early in life (e.g. the first five months, Coe 1945), especially in the second and third months after settling. Growth is also fastest when the water temperature is warmest (July) and dinoflagellate populations are high. Growth slows after 2–3 years (Coe 1945). Following settlement individuals grow 76 mm in the first year and 96 mm after two years (Haderlie and Abbott 1980). Individuals that are highest in the intertidal grow slower than those lower, and those that are continuously submerged are larger and grow faster than those exposed by tides as these individuals grow thick shells and cannot feed continuously. Faster growth is also seen for individuals in shaded areas than those in full sunlight (Haderlie and Abbott 1980). More byssal threads are grown during the night than the day and the number produced correlates with the density of mussels, salinity, and temperature (Haderlie and Abbott 1980). Shell morphology differs with wave exposure: those in wave-exposed habitats had lower shell height and width ratio and a thicker shell, more dysodont teeth, and a thicker hinge ligament (Barkley Sound, BC Canada, see Fig. 2 Akester and Martel 2000). Interestingly, sympatric species show similar shell morphology, which may be due to these environmental factors and phenotypical plasticity, in addition to hybridization (Innes and Bates 1999).

Food: *Mytilus trossulus* is a filter feeder that eats organic detritus (as small as 4–5 µm in size), as well as phyto- or zooplankton (Coe 1945; Lauringson et al. 2014). Feeding is by continual intake of water driven by ciliary currents, and selective feeding with mucus secretions or sheets that cover gills (Fox 1936). Seawater pumping rates measured by Meyhöfer (1985) were approximately 1 liter per hour per gram of individual wet weight in *M. trossulus*. They feed continually when submerged and individuals can sort particles from the water (Haderlie and Abbott 1980). Concentrating some food particles, particularly dinoflagellates (e.g., *Gonyaulax catenella*), leads to high toxicity in *M. trossulus*, as well as other filter feeding organisms (e.g. *Siliqua patula*, see description in this guide), which can be

dangerous for human consumption (Haderlie and Abbott 1980).

Predators: Known predators include *Pisaster*, *Nucella*, *Ancanthina*, *Ocenebra*, *Ceratostoma*, *Cancer antennarius*, *Pachygrapsus crassipes*, *Asterias rubens*, *Cancer irroratus*, and *Eriocheir sinensis* (Newfoundland, Canada, Lowen et al. 2013; Wójcik et al. 2015). *Ceratostoma nuttalli* bores holes into both *M. californianus* and *M. trossulus*. Other predators include *Roperia poulsoni*, *Nucella canaliculata*, and *Octopus bimaculoides* (Haderlie and Abbott 1980). *Mytilus* species are also eaten by birds and are used by humans for food and bait. *M. trossulus* is a farmed species in Europe (Haderlie and Abbott 1980) and was found in archeological sites along the western North American coast (Pleistocene, Coan and Valentich-Scott 2007; Singh and McKechnie 2015). Preferential predation by *Nucella* limits *M. trossulus* and *M. galloprovincialis* in rocky intertidal zones, as *Nucella* prefers these species to *M. californianus* (Evans and Somero 2010).

Behavior: Individuals are more mobile than *M. californianus* and "crawl" to the outer edges of clumps to avoid silt deposition (Harger 1968). Although *M. edulis* tends to aggregate with conspecifics, *M. trossulus* does not (Liu et al. 2011).

Bibliography

1. AKESTER, R. J., and A. L. MARTEL. 2000. Shell shape, dysodont tooth morphology, and hinge-ligament thickness in the bay mussel *Mytilus trossulus* correlate with wave exposure. *Canadian Journal of Zoology*. 78:240-253.
2. BAYNE, B. L. 1976. Marine mussels, their ecology and physiology. *International Biological Programme*. 10:81-120.
3. BEYNON, C. M., and D. O. F. SKIBINSKI. 1996. The evolutionary relationships between three species of mussel (*Mytilus*) based on anonymous DNA polymorphisms. *Journal of Experimental Marine Biology and Ecology*. 203:1-10.
4. BRABY, C. E., and G. N. SOMERO. 2006. Ecological gradients and relative abundance of native (*Mytilus trossulus*) and invasive (*Mytilus galloprovincialis*) blue mussels in the California hybrid zone. *Marine Biology*. 148:1249-1262.
5. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
6. BURZYNSKI, A., M. ZBAWICKA, D. O. F. SKIBINSKI, and R. WENNE. 2003. Evidence for recombination of mtDNA in the marine mussel *Mytilus trossulus* from the Baltic. *Molecular Biology and Evolution*. 20:388-392.
7. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia. *In: The Light and Smith manual: intertidal invertebrates from Central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
8. COE, W. R. 1945. Nutrition and growth of the California bay-mussel (*Mytilus edulis diegensis*). *Journal of Experimental Zoology*. 99:1-14.
9. EVANS, T. G., and G. N. SOMERO. 2010. Phosphorylation events catalyzed by major cell signaling proteins differ in response to thermal and osmotic stress among native (*Mytilus californianus* and *Mytilus trossulus*) and invasive (*Mytilus galloprovincialis*) species of mussels. *Physiological and Biochemical Zoology*. 83:984-996.
10. EVSEEV, G. A., N. K. KOLOTUKHINA, and V. A. KULIKOVA. 2011. Morphological structures of the shell of *Mytilus trossulus* and *Crenomytilus grayanus* in early ontogenesis and their importance in the taxonomy of Mytilinae (Bivalvia: Mytilidae). *Journal of the Marine Biological Association of the United Kingdom*. 91:1655-1664.
11. FIELD, I. A. 1922. Biology and economic value of the sea mussel *Mytilus edulis*. *Bulletin of the United States Bureau of Fisheries*. 38:127-259.
12. FOX, D. L. 1936. The habitat and food of the California sea mussel. 4:1-64.
13. GARDNER, J. P. A., and R. J. THOMPSON. 2001. The effects of

- coastal and estuarine conditions on the physiology and survivorship of the mussels *Mytilus edulis*, *M. trossulus* and their hybrids. *Journal of Experimental Marine Biology and Ecology*. 265:119-140.
14. GELLER, J. B. 1994. Marine biological invasions as models of dispersal: tracking secondary spread and introgressive gene flow. *California Cooperative Oceanic Fisheries Investigations Reports*. 35:68-72.
 15. —. 2007. Molecular identification, p. 32-36. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley.
 16. GELLER, J. B., J. T. CARLTON, and D. A. POWERS. 1994. PCR-based detection of mtDNA haplotypes of native and invading mussels on the northeastern Pacific coast: latitudinal pattern of invasion. *Marine Biology*. 119:243-249.
 17. GOSLING, E. M. 1992a. Genetics of *Mytilus*. *Developments in Aquaculture and Fisheries Science*. 25:309-382.
 18. —. 1992b. Systematics and geographic distribution of *Mytilus*. *Developments in Aquaculture and Fisheries Science*. 25:1-20.
 19. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 20. HARGER, J. R. E. 1968. The role of behavior traits in influencing the distribution of two species of sea mussel, *Mytilus edulis* and *Mytilus californianus*. *Veliger*. 11:45-49.
 21. HELLOU, J., and R. J. LAW. 2003. Stress on stress response of wild mussels, *Mytilus edulis* and *Mytilus trossulus*, as an indicator of ecosystem health. *Environmental Pollution*. 126:407-416.
 22. HOFMANN, G. E., and G. N. SOMERO. 1995. Evidence for protein damage at environmental temperatures: seasonal changes in levels of ubiquitin conjugates and HSP70 in the intertidal mussel *Mytilus trossulus*. *Journal of Experimental Biology*. 198:1509-1518.
 23. HUNT, H. L., and R. E. SCHEIBLING. 1996. Physical and biological factors influencing mussel (*Mytilus trossulus*, *M. edulis*) settlement on a wave-exposed rocky shore. *Marine Ecology Progress Series*. 142:135-145.
 24. INNES, D. J., and J. A. BATES. 1999. Morphological variation of *Mytilus edulis* and *Mytilus trossulus* in eastern Newfoundland. *Marine Biology*. 133:691-699.
 25. JENEWEIN, B. T., and L. A. GOSSELIN. 2013. Ontogenetic shift in stress tolerance thresholds of *Mytilus trossulus*: effects of desiccation and heat on juvenile mortality. *Marine Ecology Progress Series*. 481:147-159.
 26. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the Northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 27. KAFANOV, A. I. 1999. Some nomenclatural problems in *Mytilus edulis* (Linnaeus, 1758) group (Bivalvia: Mytilidae). *Bulletin of the Institute of Malacology Tokyo*. 3:103-114.
 28. KAFANOV, A. I., and A. L. DROZDOV. 1998. Comparative sperm morphology and phylogenetic classification of recent Mytiloidea (Bivalvia). *Malacologia*. 39:129-139.
 29. KOEHN, R. K. 1991. The genetics and taxonomy of species in the genus *Mytilus*. *Aquaculture*. 94:125-145.
 30. KOTTA, J., K. OGANJAN, V. LAURINGSON, M. PAERNOJA, A. KAASIK, L. ROHTLA, I. KOTTA, and H. ORAV-KOTTA. 2015. Establishing functional relationships between abiotic environment, macrophyte coverage, resource gradients and the distribution of *Mytilus trossulus* in a brackish non-tidal environment. *Plos One*. 10.
 31. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and

- adjacent regions. University of Washington Press, Seattle.
32. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 33. —. 2007. Orthonectida, p. 203-205. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. T. Carlton (ed.). University of California Press, Berkeley.
 34. KRISHNAKUMAR, P. K., E. CASILLAS, R. G. SNIDER, A. N. KAGLEY, and U. VARANASI. 1999. Environmental contaminants and the prevalence of hemic neoplasia (leukemia) in the common mussel (*Mytilus edulis* complex) from Puget sound, Washington, USA. *Journal of Invertebrate Pathology.* 73:135-146.
 35. KURIS, A. M. 2007. Intertidal parasites and commensals, p. 24-27. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. T. Carlton (ed.). University of California Press, Berkeley.
 36. LANDERS, S. C. 2007. Symbiotic and attached ciliated protozoans, p. 70-80. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. C. Carlton (ed.). University of California Press, Berkeley.
 37. LAURINGSON, V., J. KOTTA, H. ORAV-KOTTA, and K. KALJURAND. 2014. Diet of mussels *Mytilus trossulus* and *Dreissena polymorpha* in a brackish nontidal environment. *Marine Ecology.* 35:56-66.
 38. LIU, G., E. STAPLETON, D. INNES, and R. THOMPSON. 2011. Aggregational behavior of the blue mussels *Mytilus edulis* and *Mytilus trossulus*: a potential pre-zygotic reproductive isolation mechanism. *Marine Ecology.* 32:480-487.
 39. LOWEN, J. B., D. J. INNES, and R. J. THOMPSON. 2013. Predator-induced defenses differ between sympatric *Mytilus edulis* and *M. trossulus*. *Marine Ecology Progress Series.* 475:135-143.
 40. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 41. MALLETT, A. L., and C. E. CARVER. 1995. Comparative growth and survival patterns of *Mytilus trossulus* and *Mytilus edulis* in Atlantic Canada. *Canadian Journal of Fisheries and Aquatic Sciences.* 52:1873-1880.
 42. MARTEL, A. L., C. ROBLES, K. BECKENBACH, and M. J. SMITH. 1999. Distinguishing early juveniles of Eastern Pacific mussels (*Mytilus* spp.) using morphology and genomic DNA. *Invertebrate Biology.* 118:149-164.
 43. MCDONALD, J. H., and R. K. KOEHN. 1988. The mussels *Mytilus galloprovincialis* and *Mytilus trossulus* on the Pacific coast of North America. *Marine Biology.* 99:111-118.
 44. MCDONALD, J. H., R. SEED, and R. K. KOEHN. 1991. Allozymes and morphometric characters of three species of *Mytilus* in the northern and southern hemispheres. *Marine Biology.* 111:323-333.
 45. MEYHOFER, E. 1985. Comparative pumping rates in suspension feeding bivalves. *Marine Biology.* 85:137-142.
 46. MILLS, C. E., A. C. MARQUES, A. E. MIGOTTO, D. R. CALDER, and C. HAND. 2007. Hydrozoa: polyps, hydromedusae, and siphonophora, p. 118-168. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. C. Carlton (ed.). University of California Press, Berkeley.
 47. NIESEN, T. M. 2007. Intertidal habitats and marine biogeography of the Oregonian Province, p. 3-17. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 48. PREECE, E. P., B. C. MOORE, and F. J. HARDY. 2015. Transfer of microcystin from freshwater lakes to Puget Sound, WA and toxin accumulation in marine mussels (*Mytilus trossulus*). *Ecotoxicology and Environmental Safety.* 122:98-105.
 49. QIU, J. W., R. TREMBLAY, and E. BOURGET. 2002. Ontogenetic

- changes in hyposaline tolerance in the mussels *Mytilus edulis* and *M. trossulus*: implications for distribution. Marine Ecology Progress Series. 228:143-152.
50. RAWSON, P. D., and T. J. HILBISH. 1995. Evolutionary relationships among the male and female mitochondrial-dna lineages in the I species complex. Molecular Biology and Evolution. 12:893-901.
 51. RAWSON, P. D., K. L. JOYNER, K. MEETZE, and T. J. HILBISH. 1996. Evidence for intragenic recombination within a novel genetic marker that distinguishes mussels in the *Mytilus edulis* species complex. Heredity. 77:599-607.
 52. REISH, D. J., and J. L. AYERS, JR. 1968. Studies on the *Mutilus edulis* community in Alamitos Bay, California. Veliger. 11:250-255.
 53. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
 54. —. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
 55. RIGINOS, C., and C. W. CUNNINGHAM. 2005. Local adaptation and species segregation in two mussel (*Mytilus edulis* x *Mytilus trossulus*) hybrid zones. Molecular Ecology. 14:381-400.
 56. SARVER, S. K., and D. W. FOLTZ. 1993. Genetic population structure of a species complex of blue mussels (*Mytilus* spp.). Marine Biology. 117:105-112.
 57. SEED, R. 1992. Systematics evolution and distribution of mussels belonging to the genus *Mytilus*: an overview. American Malacological Bulletin. 9:123-137.
 58. SHANKS, A. L., and R. K. SHEARMAN. 2009. Paradigm lost? Cross-shelf distributions of intertidal invertebrate larvae are unaffected by upwelling or downwelling. Marine Ecology Progress Series. 385:189-204.
 59. —. 2011. Thread-drifting juvenile *Mytilus* spp. in continental shelf waters off Coos Bay, Oregon, USA. Marine Ecology Progress Series. 427:105-115.
 60. SINGH, G. G., and I. MCKECHNIE. 2015. Making the most of fragments: a method for estimating shell length from fragmentary mussels (*Mytilus californianus* and *Mytilus trossulus*) on the Pacific Coast of North America. Journal of Archaeological Science. 58:175-183.
 61. SMITH, J. R. 1982. A survey of endogenous dopamine and serotonin in ciliated and nervous tissues of five species of marine bivalves, with evidence for specific, high-affinity dopamine-receptors in ciliated tissue of *Mytilus californianus*. Comparative Biochemistry and Physiology C: Toxicology & Pharmacology. 71:57-61.
 62. SOO, P., and P. A. TODD. 2014. The behaviour of giant clams (*Bivalvia*: *Cardiidae*: *Tridacninae*). Marine Biology. 161:2699-2717.
 63. SUCHANEK, T. H., J. B. GELLER, B. R. KREISER, and J. B. MITTON. 1997. Zoogeographic distributions of the sibling species *Mytilus galloprovincialis* and *M. trossulus* (*Bivalvia*: *Mytilidae*) and their hybrids in the north Pacific. Biological Bulletin. 193:187-194.
 64. TAM, J. C., and R. A. SCROSATI. 2014. Distribution of cryptic mussel species (*Mytilus edulis* and *M. trossulus*) along wave exposure gradients on northwest Atlantic rocky shores. Marine Biology Research. 10:51-60.
 65. TOMANEK, L., and M. J. ZUZOW. 2010. The proteomic response of the mussel congeners *Mytilus galloprovincialis* and *M. trossulus* to acute heat stress: implications for thermal tolerance limits and metabolic costs of thermal stress. Journal of Experimental Biology. 213:3559-3574.
 66. TORO, J. E., R. J. THOMPSON, and D. J. INNES. 2002. Reproductive isolation and reproductive output in two sympatric mussel species (*Mytilus*

- edulis*, *M. trossulus*) and their hybrids from Newfoundland. *Marine Biology*. 141:897-909.
67. TURJA, R., N. HOEHER, P. SNOEIJIS, J. BARSJENE, L. BUTRIMAVICIENE, T. KUZNETSOVA, S. V. KHOLODKEVICH, M. H. DEVIER, H. BUDZINSKI, and K. K. LEHTONEN. 2014. A multibiomarker approach to the assessment of pollution impacts in two Baltic Sea coastal areas in Sweden using caged mussels (*Mytilus trossulus*). *Science of the Total Environment*. 473:398-409.
68. TURJA, R., A. SOIRINSUO, H. BUDZINSKI, M. H. DEVIER, and K. K. LEHTONEN. 2013. Biomarker responses and accumulation of hazardous substances in mussels (*Mytilus trossulus*) transplanted along a pollution gradient close to an oil terminal in the Gulf of Finland (Baltic Sea). *Comparative Biochemistry and Physiology C: Toxicology & Pharmacology*. 157:80-92.
69. VAINOLA, R., and M. M. HVILSOM. 1991. Genetic divergence and a hybrid zone between Baltic and North Sea *Mytilus* populations (Mytilidae, Mollusca). *Biological Journal of the Linnean Society*. 43:127-148.
70. VAINOLA, R., and P. STRELKOV. 2011. *Mytilus trossulus* in Northern Europe. *Marine Biology*. 158:817-833.
71. VARVIO, S. L., R. K. KOEHN, and R. VAINOLA. 1988. Evolutionary genetics of the *Mytilus edulis* complex in the North Atlantic region. *Marine Biology*. 98:51-60.
72. WOJCIK, D., M. NORMANT, B. DMOCHOWSKA, and A. FOWLER. 2015. Impact of Chinese mitten crab *Eriocheir sinensis* on blue mussel *Mytilus edulis trossulus* laboratory studies of claw strength, handling behavior, consumption rate, and size selective predation. *Oceanologia*. 57:263-270.
73. WOOD, A. R., A. R. BEAUMONT, D. O. F. SKIBINSKI, and G. TURNER. 2003. Analysis of a nuclear-DNA marker for species identification of adults and larvae in the *Mytilus edulis* complex. *Journal of Molluscan Studies*. 69:61-66.
74. ZBAWICKA, M., A. BURZYNSKI, D. SKIBINSKI, and R. WENNE. 2010. Scottish *Mytilus trossulus* mussels retain ancestral mitochondrial DNA: complete sequences of male and female mtDNA genomes. *Gene*. 456:45-53.
75. ZBAWICKA, M., A. BURZYNSKI, and R. WENNE. 2007. Complete sequences of mitochondrial genomes from the Baltic mussel *Mytilus trossulus*. *Gene*. 406:191-198.

Updated 2016

Entodesma navicula

The rock-dwelling entodesma

Phylum: Mollusca
Class: Bivalvia, Heterodonta
Order: Pholadomyoidea/ Anomalodesmata
Family: Lyonsiidae

Taxonomy: The Anomalodesmata is a well-supported monophyletic group of bivalves that has previously been regarded as a subclass (e.g., Coan and Scoot 1997; Dreyer et al. 2003), however, recently authors suggest it should no longer be designated as such and, instead, be included as a basal lineage of the Heterodonta (Harper et al. 2006; Healy et al. 2008). The generic designations within the Lyonsiidae have also been unclear historically, including as few as one and as many as twelve genera (Prezant 1980, 1981b). Lyonsiid subgeneric and specific designations are often based on variable characters (e.g., periostracal color, shell shape and sculpture) leading to several synonyms and subgenera that were abandoned altogether by Prezant (1980, 1981b). *Entodesma navicula* has been referred to by its junior synonym, *Entodesma saxicola* (Yonge 1976; Haderlie 1980; Prezant 1981b; Harper et al. 2009 and references therein) due to its morphological similarity to a species described from Japan with an older name. Based on taxonomic priority (Coan and Scott 1997; Harper et al. 2009). *Entodesma navicula* was originally described in the genus *Lyonsia*, but was later transferred to *Entodesma*, a genus designated in 1845 by Philippi.

Description

Size: Lyonsiidae is a very large bivalve family (Oldroyd 1924) and *Entodesma navicula* is one of the largest species within it, with individuals reaching 150 mm in length (Quayle 1970). The illustrated specimen (from Coos Bay) is only 60 mm in length and 40 mm in width.

Color: Shell exterior is white, but also bears abundant brown color, and transversely striated periostracum. The shell interior is pink and nacreous (i.e., pearly).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott

2007). The Pholadomyoidea are characterized by a shell that has nacreous interior and inconspicuous hinge teeth (if present at all). The Lyonsiidae are unique among the, exclusively marine, group Anomalodesmata due to their attachment to hard surfaces with byssal threads (Dreyer et al. 2003; Harper et al. 2005). *Entodesma* species are distinct within the Lyonsiidae in their habit to attach to rocks and nestle into crevices. This behavior renders their shells thick and of variable shape, and their byssus strong (Prezant 1981b, 1981c).

Body: Broadly rounded externally, and with thick shell and variable morphology. The left valve often larger and extending longer than right (Lyonsiidae, Prezant 1981b). (See Fig. 1, Morton 1981 for external anatomy (as *E. saxicola*) and Fig. 13, Prezant 1981b for general internal anatomy of *Entodesma* species)

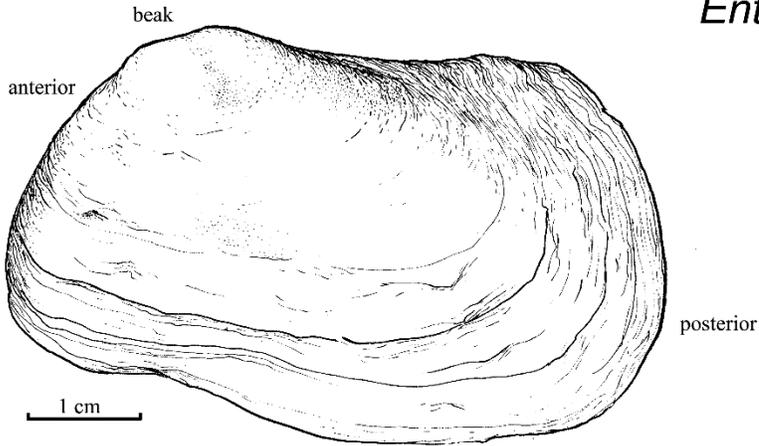
Color:

Interior: Ligament is internal (Lyonsiidae, Coan and Valentich-Scott 2007), small, extends ventrally, and is reinforced with a large lithodesma or ossicle, which is a calcareous plate (Fig. 3) (see Fig. 1, Yonge 1976). The lithodesma is only found in members of the Anomalodesmata and, it has been suggested, that its presence allows for the capacity for greater shell width, especially among the Lyonsiidae (Yonge 1976). The lithodesma is particularly large among the *Entodesma* (Prezant 1981b). A secondary dorsal ligament is sometimes observed in members of the Lyonsiidae (see Yonge 1976). Internal anatomy is described in detail by Morgan and Allen (as *E. saxicola*, 1976).

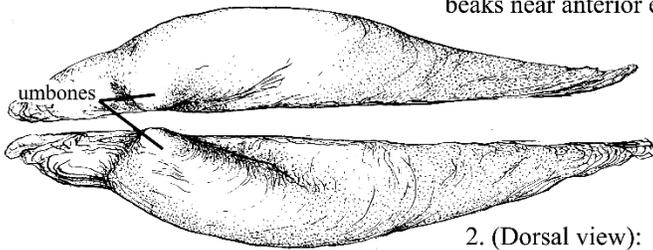
Exterior:

Byssus: Uses byssal threads to attach to substratum (e.g., floats, pilings, rock). Members of the *Entodesma* often have a byssal notch at the ventral posterior shell edge (Morgan and Allen 1976; Prezant 1981b). Byssal gland is located in the **Foot** and produces very strong byssal threads (Morgan and Allen 1976; Prezant 1981b). *Entodesma navicula* possesses a single pair

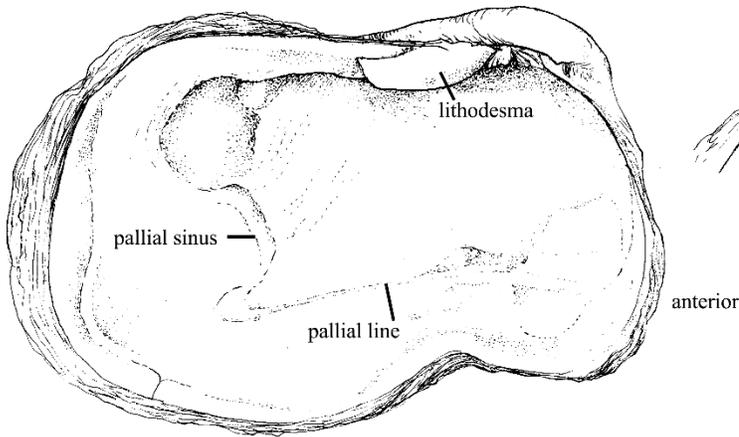
Entodesma navicula



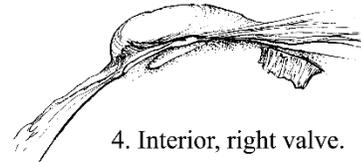
1. *Entodesma navicula* (L:60mm) x2:
shell oblong, deformed; concentric striations, rough periostracum;
beaks near anterior end, posterior truncate.



2. (Dorsal view):
beaks large, incurved; umbones not touching; posterior gaping.



3. Interior, left valve:
pearly, iridescent; hinge area without teeth of chondrophore;
lithodesma reinforces internal ligament, pallial line solid,
pallial sinus present but obscure.



4. Interior, right valve.

of byssal muscles, posteriorly, compared to other byssally attached bivalves (e.g., *Mytilus*) that possess three pairs (Morgan and Allen 1976).

Gills: Large gills are deeply plicate (i.e., folded) and comprise approximately 230 plicae (Morgan and Allen 1976).

Shell: Overall shell shape is oblong, with valves longer than they are tall, and shells can be strongly deformed due to nestling habit. The posterior is gaping and truncated. The genus *Entodesma* contains the thickest shelled species within the family Lyonsiidae. *Entodesma* and *Lyonsia* species have the capacity to adhere particles to their shell exterior, due to the presence of arenophilic radial mantle glands along the mantle edge (see **Juvenile**) (Morgan and Allen 1976; Yonge 1976; Prezant 1981b, 1981d; Lutaenko 2012). Periostracum may extend beyond the shell edges (up to 1 cm, Morgan and Allen 1976) and bear radial striations (Prezant 1981b).

Interior: (see Fig. 1, Morgan and Allen 1976.) All Lyonsiids have shell interior that is nacreous (Morgan and Allen 1976), thus, the shell interior in *E. navicula* is pearly and iridescent. The pallial line is also solid and not in patches (Coan and Valentich-Scott 2007), and the pallial sinus is obscure and angular (Oldroyd 1924) (Fig. 3). The two adductor muscle scars are conspicuous (Prezant 1981b) and of equal size (although anterior may be slightly smaller than posterior, see Prezant 1981b), but differ in shape (Fig. 3). The shell microstructure is distinct in Lyonsiid bivalves and is described for *E. navicula* by Harper et al. (2009) as homogeneous, allowing for some shell flexibility to adapt to varying substrates (Prezant 1980, 1981b, 1981c; Harper et al. 2009).

Exterior: The exterior is rough, with concentric striations, and coarse or irregular ribs (Keen and Coan 1974), but not radial ribs. The ventral margins flex, and gape and the left valve is slightly larger than right (Oldroyd 1924). The shell is brittle and breaks easily. Periostracum covers the shell exterior and is coarse and often cracks the shell as it dries, which can be prevented in collecting by applying a lubricant like Vaseline (Keen 1971).

Hinge: No true teeth or chondrophore present (Fig. 3). The beaks are large,

incurved (Oldroyd 1924), and close to anterior end (Fig. 2). The umbones do not touch (Keen and Coan 1974) (Fig. 2).

Eyes: *Entodesma* species lack photoreceptors (Prezant 1981b).

Foot: Due to their habit of attaching to various substrata, the foot is reduced, small, and cylindrical (*Entodesma*, Morgan and Allen 1976; Prezant 1981b). The foot is not used for locomotion in *E. navicula* such that it resembles *Mytilus* species (Morgan and Allen 1976).

Siphons: Siphons are short and muscular (Prezant 1981b), but not red-tipped (compare to *Hiatella arctica* description in this guide).

Burrow: Individuals do not create a burrow per se, but are often nestled into the abandoned burrows of other invertebrates (e.g., pholads).

Possible Misidentifications

There are five bivalve subclasses based on morphology and fossil evidence and one of those is the diverse Heterodonta. The monophyletic group Anomalodestmata comprises at least one sixth of all bivalve families (Harper et al. 2006), which are widely diverse and found in specific marine niches (Morgan 1981). They are characterized by a nacreous shell, a ligament with a lithodesma (ossicle), as well as a variety of characters of internal anatomy (see Dreyer et al. 2003). Family designations within this group have been difficult to interpret taxonomically due to the extreme variation in morphology and life habits of groups (see Fig. 2, Harper et al. 2006; Healy et al. 2008).

Three bivalve families including the, potentially diphyletic (see Dreyer et al. 2003) Lyonsiidae, Hiatellidae, and Thraciidae are characterized by their lack of dorsal margin ears or projecting teeth or chondrophores, and two adductor muscles. In thraciids the ligament can be both internal and external and the pallial line is continuous; in hiatellids (see *Hiatella arctica* in this guide) the ligament is always external and the pallial line is broken into patches (see below). On the other hand, in the Lyonsiids the pallial line is continuous, as in thraciids, but the ligament is always internal, unlike thraciid species (Coan and Valentich-Scott 2007).

The Lyonsiidae is a distinct family consisting up to 45 species comprising three genera (*Lyonsia*, *Entodesma*, *Mytilimeria*), with

the latter two having evolved from a *Lyonsia*-like ancestor (Prezant 1981a, 1981b; Harper et al. 2009). (For characters with which to differentiate these genera, see Prezant 1981b and 1981c) *Entodesma* species bear the thickest shell among these three genera (Prezant 1981c). Representatives of each genera occur locally, including *Mytilimeria nuttallii*, *Lyonsia californica*, *Entodesma pictum* (= *E. inflatum*), and *E. navicula* (= *E. saxicola*). *Entodesma navicula* have a thick shell and anterior end that is one third the total shell length as well as a heavy periostracum. *Entodesma pictum*, on the other hand, has a thin shell, thin periostracum and an anterior end that is less than one third the total length. The shell of *E. pictum* is also smaller, lighter in color and more regular in shape than *E. navicula*. The shell shape in *Entodesma* species is irregular due to their nestling habits and attachment to the substratum. *Mytilimeria nuttallii* has a circular shell outline. In *Lyonsia californica*, the shell and periostracum are thin and elongate with a conspicuous posterior end (Pimenta and Oliveira 2013). The latter species tends to occur in protected muddy bays and the former in the rocky intertidal among ascidians (e.g. *Cystodites*, Kabat and O'Foighil 1987; Harper et al. 2009).

Of the nestling or burrowing clams of our estuarine rocky intertidal, most of the pholads can be immediately distinguished from *Entodesma* by their file-like denticulations anteriorly, and by the two distinct sections of each valve (see *Penitella penita*, *Zirfaea pilsbryi* in this guide). The nestling habit of some clams can distort shell shape and make identification difficult (see *Protothaca staminea* in this guide).

Species from other bivalve families that may be confused with *E. navicula* include *Hiatella arctica*, *Petricola carditoides*, and *Platyodon cancellatus*. *Hiatella arctica* (= *Saxicava*) is a very similar, often deformed nestling clam. It can be most easily distinguished from *E. navicula* by its white, porcelain-like interior (Keen and Coan 1974) (not pink and pearly), and by its broken pallial line (see Plate 429B, Coan and Valentich-Scott 2007). It also has very distinctive red-tipped siphons (Kozloff 1993), which are not found in *E. navicula*. *Petricola carditoides* has an external ligament and 2–3 cardinal hinge teeth, as well as some radial sculpture, and lives in pholad burrows. It is chalky

white, with purple-tipped siphons (Kozloff 1993), and usually is narrower posteriorly than anteriorly. A myid clam, *Platyodon cancellatus*, is another rock dweller, but it is a burrower, not a nestler (Quayle 1970; Coan and Valentich-Scott 2007). It has a chondrophore and tooth in its hinges, fine, almost lamellar concentric exterior sculpture, and a white interior with a well-developed pallial sinus (Kozloff 1974).

Juveniles of the families Clavagellidae and Penicillidae (“watering pot bivalves”) are morphologically similar to members of the Lyonsiidae (Morton 2007).

Ecological Information

Range: Type locality is Vancouver Island, British Columbia (as *E. saxicola*, Dall 1916). Known range extends in the north Pacific in the Kurile Islands and northern Japan down through the Aleutian Islands in Alaska to San Diego, California (Harper et al. 2009).

Local Distribution: Local distribution includes sites in Coos Bay, including Fossil Point.

Habitat: Occurs among rocks and in crevices and abandoned pholad burrows. Individuals also found attached by byssus to floats and pilings.

Salinity: Collected at salinities of 30.

Temperature:

Tidal Level: Intertidal and subtidal to 60, or even 82 meters deep (Keen and Coan 1974; Harper et al. 2009).

Associates: Co-occurs with other nestling and burrowing molluscs (e.g., *Hiatella*, *Zirfaea*, *Penitella*).

Abundance: Common in Puget Sound, Washington. Individuals are present, but not common, in Oregon (Quayle 1970).

Life-History Information

Reproduction: All members of the Anomalodesmata are believed to be hermaphroditic (Healy et al. 2008).

Entodesma navicula is a hermaphroditic species, with external fertilization and planktonic larvae. Eggs and sperm are emitted alternatively (Quayle 1970). Although the development of this species has not been described, other members of the Anomalodesmata are free-spawners, primarily in summer months. These include *Lyonsia bracteata*, which is a simultaneous hermaphrodite with oocytes that are 120 µm

and surrounded by a thick egg jelly; *Mytilimeria nuttallii*, is also a simultaneous hermaphrodite that free-spawns in July with oocytes that are also 120 µm in diameter (Kabat and O'Foighil 1987). The sperm morphology of the family Lyonsiidae is of modified (or elongated) morphology (see Fig. 6, Healy et al. 2008). Ova have been observed within the suprabranchial chamber of the gills in several *Entodesma* species and larvae have a short pelagic duration (Prezant 1981b).

Larva: Larval development has not been described for *E. navicula*.

Juvenile:

Longevity: Arenophilic mantle glands (which produce a secretion that allows for material to be adhered to shell surface, over the periostracum, Morton 1987) are often present in juvenile *Entodesma* species, but these are usually lost by adulthood, shell thickness increases (Prezant 1981b). These glands develop within the mantle, but the specific location has been debated (either the outer fold (Prezant 1981c, 1981d) or the middle and inner folds (Morton 1987)), and secrete shell through the periostracum.

Growth Rate:

Food: A suspension feeder. Ciliary currents move water across gills and all incoming particles move toward the ventral margin of the inner demibranch before they move anteriorly to the mouth (Yonge 1952; see Fig. 4, Morgan and Allen 1976).

Predators:

Behavior: Individuals adapt to their particular rocky niche by changing shell shape with grows, leading to shells with highly irregular morphology.

Bibliography

1. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
2. COAN, E. V., and P. H. SCOTT. 1997. Checklist of the marine bivalves of the northeastern Pacific Ocean. Santa Barbara Museum of Natural History Contributions in Science. 1:1-28.
3. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In*:
4. DALL, W. H. 1916. A review of some bivalve shells of the group Anatinacea from the west coast of America. Proceedings of the United States National Museum. 49:441-456.
5. DREYER, H., G. STEINER, and E. M. HARPER. 2003. Molecular phylogeny of Anomalodesmata (Mollusca : Bivalvia) inferred from 18S rRNA sequences. Zoological Journal of the Linnean Society. 139:229-246.
6. HARPER, E. M., A. G. CHECA, and A. B. RODRIGUEZ-NAVARRO. 2009. Organization and mode of secretion of the granular prismatic microstructure of *Entodesma navicula* (Bivalvia: Mollusca). Acta Zoologica. 90:132-141.
7. HARPER, E. M., H. DREYER, and G. STEINER. 2006. Reconstructing the Anomalodesmata (Mollusca : Bivalvia): morphology and molecules. Zoological Journal of the Linnean Society. 148:395-420.
8. HEALY, J. M., R. BIELER, and P. M. MIKKELSEN. 2008. Spermatozoa of the Anomalodesmata (Bivalvia, Mollusca) with special reference to relationships within the group. Acta Zoologica. 89:339-350.
9. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In*: Reproduction and development of marine invertebrates of the northern Pacific Coast. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
10. KEEN, A. M. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. Stanford University Press, Stanford, CA.
11. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
12. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and

- adjacent regions. University of Washington Press, Seattle.
13. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 14. LUTAENKO, K. A. 2012. Transportation of bivalve shells with attached algae in Ussuriysky Bay (Sea of Japan). Byulleten' Dal'nevostochnogo Malakologicheskogo Obshchestva. 15-1:154-164.
 15. MORGAN, R. E., and J. A. ALLEN. 1976. On the functional morphology and adaptations of *Entodesma saxicola* (Bivalvia, Anomalodesmacea). Malacologia. 15:233-240.
 16. MORTON, B. 1981. The Anomalodesmata. Malacologia. 21:35-60.
 17. —. 1987. The mantle margin and radial mantle glands of *Entodesma saxicola* and *Entodesma inflata* (Bivalvia, Anomalodesmata, Lyonsiidae). Journal of Molluscan Studies. 53:139-151.
 18. —. 2007. Evolution of the watering pot shells (Bivalvia: Anomalodesmata: Clavagellidae and Penicillidae). Records of the Western Australian Museum. 24:19-64.
 19. OLDROYD, I. S. 1924. Marine shells of Puget Sound and vicinity. University of Washington Press, Seattle.
 20. PIMENTA, A. D., and C. D. DE CASTRO OLIVEIRA. 2013. Taxonomic review of the genus *Lyonsia* (Pelecypoda: Lyonsiidae) from east coast of South America, with description of a new species and notes on other western Atlantic species. American Malacological Bulletin. 31:75-84.
 21. PREZANT, R. S. 1980. Taxonomic revisions of marine Lyonsiidae bivalvia. Bulletin of the American Malacological Union. 46:75-75.
 22. —. 1981a. Arenophilic mantle glands, shell ultrastructure, taxonomy, and evolution of the Lyonsiidae (Bivalvia: Anomalodesmata). Vol. Ph.D. University of Delaware.
 23. —. 1981b. Comparative shell ultrastructure of Lyonsiid bivalves. Veliger. 23:289-299.
 24. —. 1981c. Taxonomic re-evaluation of the bivalve family Lyonsiidae. Nautilus. 95:58-72.
 25. —. 1981d. The Arenophilic radial mantle glands of the Lyonsiidae (Bivalvia, Anomalodesmata) with notes on Lyonsiid evolution. Malacologia. 20:267-289.
 26. QUAYLE, D. B. 1970. The intertidal bivalves of British Columbia. British Columbia Provincial Museum, Victoria, BC, Canada.
 27. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides: an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford University Press, Stanford.
 28. YONGE, C. M. 1976. Primary and secondary ligaments with the *Lithodesma* in the Lyonsiidae (Bivalvia, Pandoracea). Journal of Molluscan Studies. 42:395-408.

Updated 2016

Clinocardium nuttallii

Basket or heart cockle

Phylum: Mollusca
Class: Bivalvia, Heterodonta
Order: Veneroida
Family: Cardiidae

Taxonomy: This species was originally described as *Cardium nuttallii* (named after the zoologist, Thomas Nuttall) by Conrad in 1837. *Cardium* was later split into several groups and *C. nuttallii* was moved to the genus *Clinocardium*, which was designated by Keen in 1936 (Kafanov 1980; Schneider 2002). Other known synonyms include *Cardium californianum* and *Cardium corbis* (e.g. Fraser 1931; Weymouth and Thompson 1931). The distinctive shell morphology of *Clinocardium* (with some associated subgenera, see Kafanov 1980) is distinct within the subfamily Clinocardiinae (Karanov 1980). Taxonomy of the group is based largely on stomach and shell morphology (Schneider 1994, 1995).

Description

Size: Individuals up to 72 mm (Packard 1918), but often grows to greater size, particularly on northern beaches (Fraser 1931), where they can be up to 100 mm (Kozloff 1993).

Color: Warm brown when young and mottled. Adults are light brown (Kozloff 1993).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Cariids have distinctly inflated shells and central beaks, which is not seen in any other bivalve family (Kozloff 1993; Coan and Valentich-Scott 2007).

Body: (see Fig. 298, Kozloff 1993)

Color:

Interior: Ligament is entirely dorsal, and not internal. Labial palps are triangular and consist of 30 ridges. The complex intestine is with 11 loops and the total length (from crystalline style to exit from visceral mass) is 300 mm (Schneider 1994). For diagram of internal anatomy see Schneider 1994.

Exterior:

Byssus:

Gills: Gills are filibranch type, and are strongly plicated and fused to a siphonal septum posteriorly (Bernard and Noakes 1990; Schneider 1994). The outer demibranch bears 53–120 plicae (each plica comprises 40 filaments), while the inner has 75–110 (Schneider 1994). The gills in many suspension feeding bivalves are elongated and folded to increase filtering surface area (Bernard and Noakes 1990).

Shell: When viewed from the side (left or right valve), the shell is triangular, but when viewed from either end it is heart-shaped (Fig. 3) (hence “heart cockle”, Kozloff 1993). Usually approximately 34 ribs radiate outward from the shell umbo (fig. 1) and are crossed with concentric growth lines (Haderlie and Abbott 1980).

Interior: White, but not pearly. The anterior and posterior muscle scars equal in area (compare to *Adula californiensis*, this guide) and pallial line is simple. Known for its large foot and short siphon. Shell of *C. californiense* is composed of three layers including an inner layer that is cross-laminar, middle complex cross laminar, and outer that is prismatic in structure (Zhang et al. 2014).

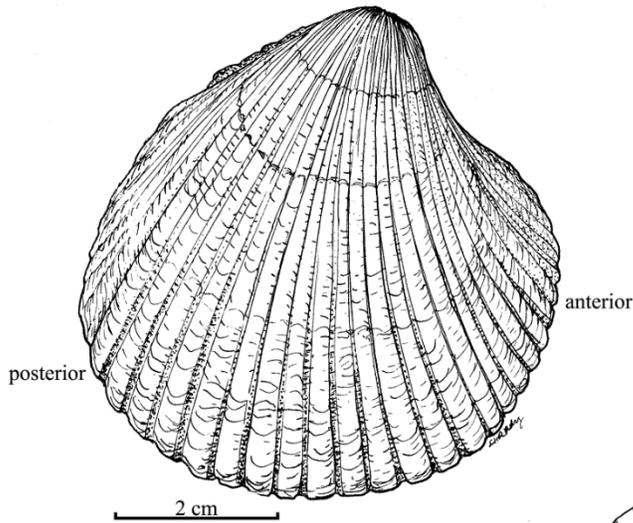
Exterior: Shell as high as long (Kozloff 1974), or higher with individuals generally longer than wide during first year (Length: anterior to posterior) (Fraser 1931). Valves are alike, and shell is inflated, triangular, and with rounded corners (Kozloff 1974). Shell thick, but rather brittle (Keep and Longstreth 1935). The posterior end is evenly rounded and smooth. The umbones are prominent (Abbott 1968), beaks nearly central and directed anteriorly (Keen and Coan 1974) (Fig. 2).

Hinge: Hinge is central, with one strong cardinal tooth, and an anterior and posterior lateral tooth in each valve (Fig. 2).

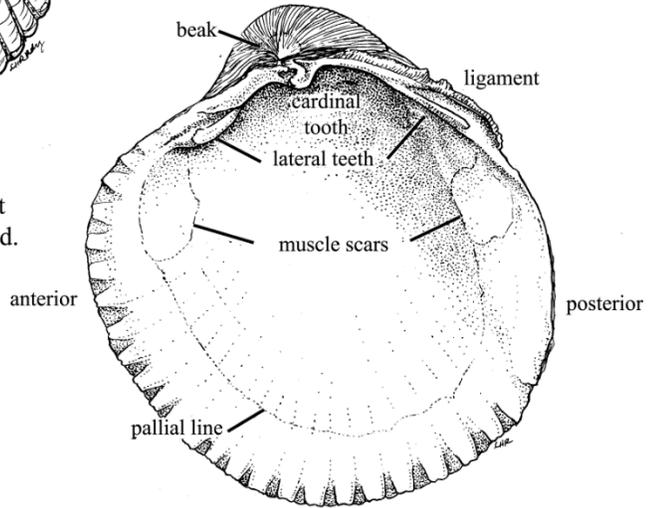
Eyes: Bears numerous, tiny eyes on optical tentacles on mantle margin (Haderlie and Abbott 1980).

Foot: Foot enables excellent digging (Ricketts and Calvin 1952; Coan and Valentich-Scott 2007). The large and strong

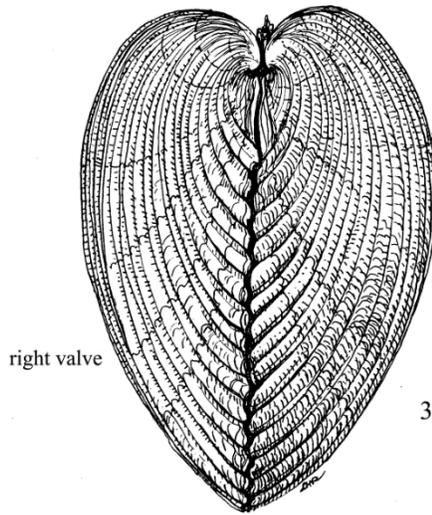
Clinocardium nuttallii



1. *Clinocardium nuttallii*, right valve 1.5x:
5.8cm, about 35 strong radial ribs; height
greater than width; shell inflated, rounded.



2. Interior, right valve:
beaks nearly central, directed anteriorly;
surface white; scars equal, pallial line simple;
one cardinal, two lateral teeth; ligament
external.



3. Profile (anterior end):
heart-shaped.

foot can be used to push and flip the entire body (e.g., to escape predation from *Pycnopodia helianthoides*, Kozloff 1993; *Pisaster brevispinus*, Haderlie and Abbott 1980).

Siphons: No siphon tubes. Instead, siphons are simply holes in the mantle margin that allow for only a shallow burrow (Ricketts and Calvin 1952). *Clinocardium nuttallii* has 60 mantle tentacles, which are largely present dorsal to the excurrent siphon opening and extend to top of posterior adductor muscles (Schneider 1994).

Burrow: Shallow burrow is within 1 mm of surface (Ricketts and Calvin 1952; Chang and Levings 1989), so that the posterior end of the individual is situated just below the sediment (Kozloff 1993). Burrowing time is slowed (up to two-fold) in sediments bearing seagrass roots and/or invertebrate tubes (Brenchley 1982), however, a greater density of *C. nuttallii* was observed in mudflats that had eelgrass (*Zostera marina*) than those that did not (Galleher et al. 2012). If buried less than 50 mm (e.g., by dredging), *C. nuttallii* can open its siphon to filter feed after 24 hrs (Chang and Levings 1989).

Possible Misidentifications

The taxonomy (especially among higher-level taxa) of family Cardiidae, or cockles, has been thoroughly studied due to the diverse morphology and good fossil record (see Schneider 1992, 1994, 1995, 2002). It contains one to four species locally and *C. nuttallii* is the only species included in most recent keys (Coan and Valentich-Scott 2007). The family is within the Hederodonta and, as such, possesses few hinge teeth and is characterized by ovate and inflated shells with central beaks, hinges with lateral teeth, shell sculpture that is with radial ribs, a hinge ligament that is entirely external (see Plate 397B, Coan and Valentich-Scott 2007). They have shells that are generally not cemented to the substratum and a dorsal margin that is without ears (Coan and Valentich-Scott 2007). No other bivalve family has such an inflated shell and central beaks.

Clinocardium blandum is an offshore species, with distribution from Sonoma county, California northward, *Nemocardium centifilosum* is also an offshore species and *Trachycardium quadragenarium* is a southern species, known from southern California to

Monterey, California (Coan and Valentich-Scott 2007). *Nemocardium*, with few extant species, has a prominent shell sculpture, with posterior ribs only and an otherwise smooth surface (see Fig. 5, ter Poorten 2013).

Ecological Information

Range: Type locality is the Columbia River estuary in Oregon. Japan, Alaska and south along Pacific coast to San Diego (Weymouth and Thompson 1931; Haderlie and Abbott 1980). Fossils from the family Cardiidae are found along the north Pacific and European subarctic, and date to the Cenozoic (Kafanov 1980).

Local Distribution: Local distribution near bay mouths on tideflats in most Oregon estuaries as well as on exposed beaches south of Oregon (Weymouth and Thompson 1931).

Habitat: Beaches of uniform, but not very coarse sand (Fraser 1931; "corn meal sand", Packard 1918; Ricketts and Calvin 1952). Often found in exposed beaches.

Clinocardium nuttallii occur in diverse habitats from exposed sandy beaches to fine bay sand (Fraser 1931), and large populations can be found in eelgrass/mud areas (Kozloff 1993).

Salinity: Not found in upper bays where salinities vary greatly.

Temperature:

Tidal Level: High and mid intertidal to deep waters, up to 200 m offshore in sandy areas or bays (Haderlie and Abbott 1980; Coan and Valentich-Scott 2007).

Associates: Small specimens are often host to young *Pinnixa faba* or *P. littoralis* (pea crabs) (Ricketts and Calvin 1971; Haderlie and Abbott 1980). Mantle, siphon, and foot tissue of individuals older than two years, found to house the green endosymbiotic alga, zoochlorellae (e.g. *Chlorella*), with a commensal or parasitic relationship suggested (Cooke 1975; Hartman and Pratt 1976; Jones and Jacobs 1992; Soo and Todd 2014).

Abundance: Not as abundant as other mollusks (e.g., *Saxidomus*, *Protothaca*, British Columbia, Canada, Fraser 1931). This species is the most abundant of its family on the west coast (Keep and Longstreth 1935). Abundant at Garrison Bay, Washington from -0.61 to +0.92 meters, with approximately 5–13 cockles per square meter (Gallucci and Galluci 1982). In a comparison of abundance

relative to other bay clams in two Oregon estuaries, *C. nuttallii* was found to be twice as abundant (Netarts Bay) and 7–9 times more abundant (Tillamook Bay) in subtidal than intertidal habitats (D'Andrea et al. 2015).

Life-History Information

Reproduction: Simultaneous hermaphroditism has been observed in this species (Edmondson 1920; Fraser 1931; Gallucci and Gallucci 1982). Spawning occurs annually from June–Oct in Oregon, April–Nov in San Juan Island (Haderlie and Abbott 1980; Garrison Bay, Gallucci and Gallucci 1982; Yaquina and Tillamook Bays, Oregon, Robinson and Breese 1982; Kabat and O'Foighil 1987), and June and July in British Columbia, Canada (Fraser 1931). Oocytes are 80 μm in diameter and are surrounded by a jelly layer that is 50 μm thick. Sperm are motile for up to 2 hours (at 4°C, Liu et al. 2008). Complete description of gametogenesis see Gallucci and Gallucci 1982.

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the “D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone. Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig. 1, Kabat and O'Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001). At 15°C in the laboratory, development proceeds as follows: first cleavage after 1 hour, ciliated blastula at 10 hours, and early free-swimming veliger larvae after 18 hours (Kabat and O'Foighil 1987; Brink 2001). Early embryonic development stops at temperatures below 2.8°C (Liu et al. 2008). Larval growth increases with

increasing temperature, but temperatures above 26.3°C are lethal (Liu et al. 2010).

Juvenile: Sexual maturity reached at 2 years (Haderlie and Abbott 1980; Gallucci and Gallucci 1982).

Longevity: 7 to 16 years (Fraser 1931; Weymouth and Thompson 1931; Haderlie and Abbott 1980).

Growth Rate: Northern populations, in contrast to southern, show a slower initial but more sustained growth, and reach the greater age and larger size (Weymouth and Thompson 1931). Annual growth rings are obvious, especially in northern specimens with cold winters, when growth is very slow. Shells may also show a growth pattern that correlates with tidal cycles. Bands or rings that are widely spaced are developed after spring tides and dense bands during neap times, when cockles experience more aerial exposure (Evans 1972; Haderlie and Abbott 1980). Shell growth lines (which are visible internally and externally) are added annually, beginning in later summer to early fall, with more faster growth occurring with warmer water temperature and more food (Svalbard, Ambrose et al. 2012). Growth is effected by several biotic and abiotic factors (e.g., ice cover in Svalbard, Tallqvist and Sundet 2000). First year cockles were approximately 34–50 mm in length, second year were 54–70, and third year 65–77 in Garrison Bay, San Juan Island, Washington (Gallucci and Gallucci 1982; Liu et al. 2010).

Food: Suspension feeders, *C. nuttallii* strain material through their gills, by pumping water through the pallial cavity using cilia that covers gill surfaces (Bernard and Noakes 1990). *Clinocardium nuttallii* can pump a volume of 2.51 liters per hour per gram body weight (Bernard and Noakes 1990). Although suspension and filter feeding can have a negative effect on larval settlement, settlement was not impeded by the siphonal current of *C. nuttallii* (Ertman and Jumars 1988). Ingests larvae of other marine invertebrates (e.g., *Lepeophtheirus salmonis*, Webb et al. 2013). Pumping rates measured by Meyhofer (1985) were approximately 0.14 cubic centimeters per second per square centimeter unit gill area.

Predators: Known predators include sea otters (*Enhydra lutris nereis*, Kannan et al. 2004), sea stars (*Pycnopodia helianthoides*), birds, humans (e.g., First Nations, Liu et al.

2004; Lui et al. 2008), octopus, (*Octopus dofleini*, Hartwick et al. 1981). *Clinocardium nuttallii* tend to be “easy” prey, as they are often found on the surface of tide flats. As planktonic larvae, *C. nuttallii* are preyed upon by planktonic predators and suspension feeders. The life-history of *Clinocardium nuttallii* has undergone recent investigation into aquaculture potential in the northeast Pacific (e.g., Liu et al. 2010; Epelbaum et al. 2011; Dunham et al. 2013a, b).

Behavior: Can be very active, flipping to avoid predation with their large muscular foot and digging quickly. However, individuals do not burrow deeply or laterally.

Bibliography

1. ABBOTT, R. T. 1968. Seashells of North America; a guide to field identification. Golden Press, New York.
2. AMBROSE, W. G., P. E. RENAUD, W. L. V. LOCKE, F. R. COTTIER, J. BERGE, M. L. CARROLL, B. LEVIN, and S. RYAN. 2012. Growth line deposition and variability in growth of two circumpolar bivalves (*Serripes groenlandicus*, and *Clinocardium ciliatum*). *Polar Biology*. 35:345-354.
3. BERNARD, F. R., and D. J. NOAKES. 1990. Pumping rates, water pressures, and oxygen use in eight species of marine bivalve mollusks from British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*. 47:1302-1306.
4. BRENCHLEY, G. A. 1982. Mechanisms of spatial competition in marine soft-bottom communities. *Journal of Experimental Marine Biology and Ecology*. 60:17-33.
5. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
6. CHANG, B. D., and C. D. LEVINGS. 1978. Effects of burial on the heart cockle *Clinocardium nuttallii* and the Dungeness Crab *Cancer magister*. *Estuarine and Coastal Marine Science*. 7:409-412.
7. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
8. COOKE, W. J. 1975. The occurrence of an endozoic green alga in the marine mollusk *Clinocardium nuttallii*. *Phycologia*. 14:35-40.
9. D'ANDREA, A. F., E. A. PEROTTI, S. GALLEHER, C. L. MOFFETT, and S. A. STRICKLAND. 2015. Can subtidal bay clams serve as source populations for the intertidal? A preliminary evaluation of the subtidal "spawning stock hypothesis" in two Oregon estuaries. *Journal of Shellfish Research*. 34:623-623.
10. DUNHAM, A., H. GURNEY-SMITH, N. PLAMONDON, S. YUAN, and C. M. PEARCE. 2013a. Aquaculture potential of the basket cockle (*Clinocardium nuttallii*). Part 1: effects of stocking density on first year grow-out performance in intertidal and off-bottom suspended culture. *Aquaculture Research*. 44:1236-1253.
11. —. 2013b. Aquaculture potential of the basket cockle (*Clinocardium nuttallii*). Part 2: effects of stocking density and depth on second year grow-out performance of three size cohorts in intertidal and off-bottom suspended culture. *Aquaculture Research*. 44:1277-1299.
12. EDMONDSON, C. H. 1920. Edible mollusca of the Oregon coast. *Occasional papers of the Bernice Pauahi Bishop Museum of Polynesian Ethnology and Natural History*. 7:179-201.
13. EPELBAUM, A., C. M. PEARCE, S. YUAN, N. PLAMONDON, and H. GURNEY-SMITH. 2011. Effects of stocking density and substratum on the survival, growth, burrowing behaviour and shell morphology of juvenile basket cockle, *Clinocardium nuttallii*: implications for nursery seed production and field outplanting. *Aquaculture Research*. 42:975-986.
14. ERTMAN, S. C., and P. A. JUMARS. 1988. Effects of bivalve siphonal currents on the settlement of inert

- particles and larvae. *Journal of Marine Research*. 46:797-813.
15. EVANS, J. W. 1972. Tidal growth increments in the cockle *Clinocardium nuttalli*. *Science*. 176:416-4177.
 16. FRASER, C. M. 1931. Notes on the ecology of the cockle, *Cardium corbis* Martyn. *Transactions of the Royal Society of Canada, Section V, Biological Sciences, Third Series*. 25:59-72.
 17. GALLEHER, S. Y., A. D'ANDREA, A. HUTMACHER, and E. I. RIEDLECKER. 2012. Key habitat factors structuring clam communities in Tillamook Bay, OR USA. *Journal of Shellfish Research*. 31:287-287.
 18. GALLUCCI, V. F., and B. B. GALLUCCI. 1982. Reproduction and ecology of the hermaphroditic cockle *Clinocardium nuttallii* (Bivalvia, Cardiidae) in Garrison Bay. *Marine Ecology Progress Series*. 7:137-145.
 19. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 20. HARTMAN, M. C., and I. PRATT. 1976. Infection of heart cockle, *Clinocardium nuttallii*, from Yaquina Bay, Oregon, with an endosymbiotic alga. *Journal of Invertebrate Pathology*. 28:291-299.
 21. HARTWICK, B., L. TULLOCH, and S. MACDONALD. 1981. Feeding and growth of octopus *Dofleini* (Wulker). *Veliger*. 24:129-138.
 22. JI, H. M., W. Q. ZHANG, and X. W. LI. 2014. Fractal analysis of microstructure-related indentation toughness of *Clinocardium californiense* shell. *Ceramics International*. 40:7627-7631.
 23. JONES, D. S., and D. K. JACOBS. 1992. Photosymbiosis in *Clinocardium nuttallii* implications for tests of photosymbiosis in fossil molluscs. *Palaios*. 7:86-95.
 24. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 25. KAFANOV, A. I. 1980. Systematics of the subfamily Clinocardiinae Kafanov, 1975 (Bivalvia, Cardiidae). *Malacologia*. 19:297-328.
 26. KANNAN, K., N. KAJIWARA, M. WATANABE, H. NAKATA, N. J. THOMAS, M. STEPHENSON, D. A. JESSUP, and S. TANABE. 2004. Profiles of polychlorinated biphenyl congeners, organochlorine pesticides, and butyltins in southern sea otters and their prey. *Environmental Toxicology and Chemistry*. 23:49-56.
 27. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
 28. KEEP, J., and J. LONGSTRETH. 1935. West coast shells: a description in familiar terms of the principal marine, fresh-water, and land mollusks of the United States, British Columbia, and Alaska, found west of the Sierra. Stanford University Press, Stanford, CA.
 29. KOZLOFF, E. N. 1974a. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
 30. —. 1974b. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago and adjacent Regions. University of Washington Press, Seattle and London.
 31. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 32. LIU, W., A. O. ALABI, and C. M. PEARCE. 2008. Fertilization and embryonic development in the basket cockle, *Clinocardium nuttallii*. *Journal of Shellfish Research*. 27:393-397.
 33. LIU, W., H. GURNEY-SMITH, A. BEERENS, and C. M. PEARCE. 2010. Effects of stocking density, algal density, and temperature on growth and survival of larvae of the basket

- cockle, *Clinocardium nuttallii*. Aquaculture. 299:99-105.
34. LUTAENKO, K. A. H., VIRGINIE. 2011. TYPE MATERIAL OF BIVALVE MOLLUSKS COLLECTED DURING VENUS VOYAGE (1836-1839) FROM KAMCHATKA, RUSSIA, IN THE MUSEUM NATIONAL D'HISTOIRE NATURELLE, PARIS. Malacologia. 54:77-85.
 35. MEYHOFER, E. 1985. Comparative pumping rates in suspension feeding bivalves. Marine Biology. 85:137-142.
 36. PACKARD, E. L. 1918. Molluscan fauna from San Francisco Bay. Zoology. 14:199-452.
 37. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
 38. —. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
 39. ROBINSON, A. M., and W. P. BREESE. 1982. The spawning season of four species of clams in Oregon. Journal of Shellfish Research. 2:55-57.
 40. SCHNEIDER, J. A. 1992. Preliminary cladistic analysis of the bivalve family Cardiidae. American Malacological Bulletin. 9:145-155.
 41. —. 1994. On the anatomy of the alimentary tracts of the bivalves *Nemocardium* (Keenaea), *Centifilosum* (Carpenter, 1864) and *Clinocardium nuttallii* (Conrad, 1837) (Cardiidae). Veliger. 37:36-42.
 42. —. 1995. Phylogeny of the Cardiidae (Mollusca, Bivalvia): Protocardiinae, Laevicardiinae, Lahilliinae, Tulongocardiinae subfam n and Pleuriocardiinae subfam n. Zoologica Scripta. 24:321-346.
 43. —. 2002. Phylogeny of cardiid bivalves (cockles and giant clams): revision of the Cardiinae and the importance of fossils in explaining disjunct biogeographical distributions. Zoological Journal of the Linnean Society. 136:321-369.
 44. SOO, P., and P. A. TODD. 2014. The behaviour of giant clams (Bivalvia: Cardiidae: Tridacninae). Marine Biology. 161:2699-2717.
 45. TALLQVIST, M. E., and J. H. SUNDET. 2000. Annual growth of the cockle *Clinocardium ciliatum* in the Norwegian Arctic (Svalbard area). Hydrobiologia. 440:331-338.
 46. TER POORTEN, J. J. 2013. Revision of the recent species of the genus *Nemocardium* Meek, 1876 (Bivalvia, Cardiidae), with the descriptions of three new species. Basteria. 77:45-73.
 47. VIDAL, J. 1999. Taxonomic review of the elongated cockles: genera *Trachycardium*, *Vasticardium* and *Acrosterigma* (Mollusca, Cardiidae). Zoosystema. 21:259-335.
 48. WEBB, J. L., J. VANDENBOR, B. PIRIE, S. M. C. ROBINSON, S. F. CROSS, S. R. M. JONES, and C. M. PEARCE. 2013. Effects of temperature, diet, and bivalve size on the ingestion of sea lice (*Lepeophtheirus salmonis*) larvae by various filter-feeding shellfish. Aquaculture. 406:9-17.
 49. WEYMOUTH, F. W., and S. H. THOMPSON. 1931. The age and growth of the Pacific cockle (*Cardium corbis*, Martyn). Bulletin, U.S. Bureau of Fisheries. 46:633-641.

Updated 2016

Corbicula fluminea

The Asian clam

Phylum: Mollusca
Class: Bivalvia, Heterodonta
Order: Veneroida
Family: Corbiculidae

Taxonomy: *Corbicula fluminea* was originally described as one of three species in the genus *Tellina* (Araujo et al. 1993). The taxonomy of this group was based on shell morphology and color, which are variable characters (Sousa et al. 2008a), and has led to the synonymization of several previously described species that were found to display intraspecific variation (Araujo et al. et al. 1993). *Corbicula fluminea* was synonymized with *C. fluviatilis* by Prashad in 1929, *C. manilensis* in 1933 (Talvera and Faustino in Britton and Morton 1979) and *C. leana* by Morton (1977). This synonymization led to two *Corbicula* species with widespread distribution: *C. fluminea* (a freshwater species) and *C. fluminalis* (an estuarine species) (Araujo et al. et al. 1993 but see Sousa et al. 2008a). These species can be further distinguished by geographic location and characters of biology and morphology, as all North American populations were determined to be only *C. fluminea* (see Britton and Morton 1979; Morton 1982; Araujo et al. et al. 1993).

Description

Size: Individuals range in size from less than 2.5– 6.4 cm in length, and are rarely over 5.0 cm (Ward and Whipple 1963). Individuals over 40 mm in length are often found in canal bottoms (Eng 1979). The illustrated specimen (from the Columbia River) is 14 mm in length. Mean wet weight for *C. fluminea* from the Potomac River were estimated for year classes 1, 2, 3, and 4 to be 0.48, 1.47, 4.30, and 10.37 grams, respectively (Cohen et al. 1984).

Color: Tan exterior; the shell interior is white, smooth, polished, and is sometimes with purple markings (Britton and Morton 1979). A periostracum is present and thick (Coan and Valentich-Scott 2007), particularly in canal specimens; specimens from earth-lined habitats may lack periostracum (Eng 1979).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves

or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). The Veneroida is a large and diverse bivalve heterodont order that is characterized by well developed hinge teeth. There are 22 local families, and members of the Corbiculidae have an elongated hinge and serrate teeth laterally, *C. fluminea* is common in freshwater habitats and has a conspicuous triangular shape with low commarginal ridges (see Plate 398B, 415E, Coan and Valentich-Scott 2007).

Body:

Color:

Interior: The ligament is thick and strong, and is entirely external and posterior to the beaks (Fig. 2).

Exterior:

Byssus: A small byssus is present only in first year (Morton 1979a) (not figured).

Gills:

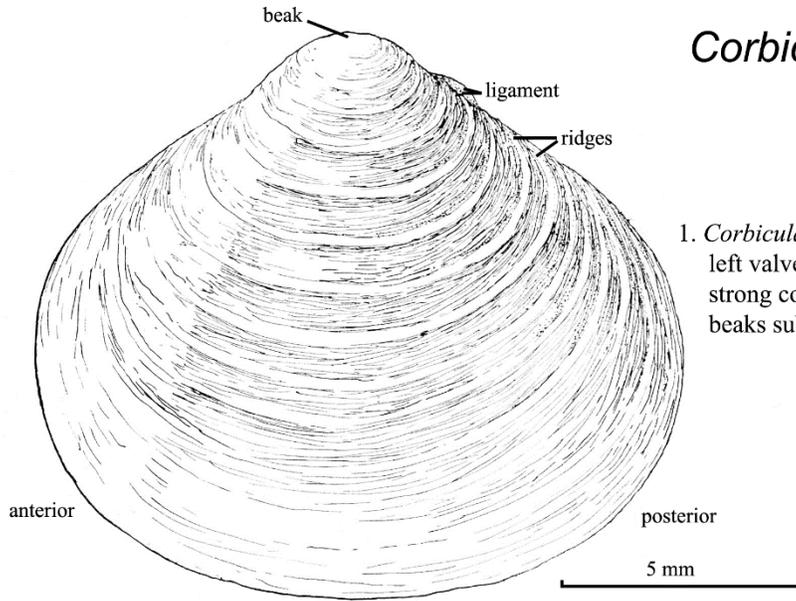
Shell: The overall shell shape is triangular (Coan and Valentich-Scott 2007) to subcircular. Both valves are similar and regular, and the shell is thick.

Interior: The adductor muscle scars are approximately equal (Coan and Valentich-Scott 2007) (Fig. 3). The pallial line is incomplete anteriorly (Corbiculidae, Britton and Morton 1979).

Exterior: The exterior sculpture has heavy concentric ridges and faint growth rings (Britton and Morton 1979) (Fig. 1).

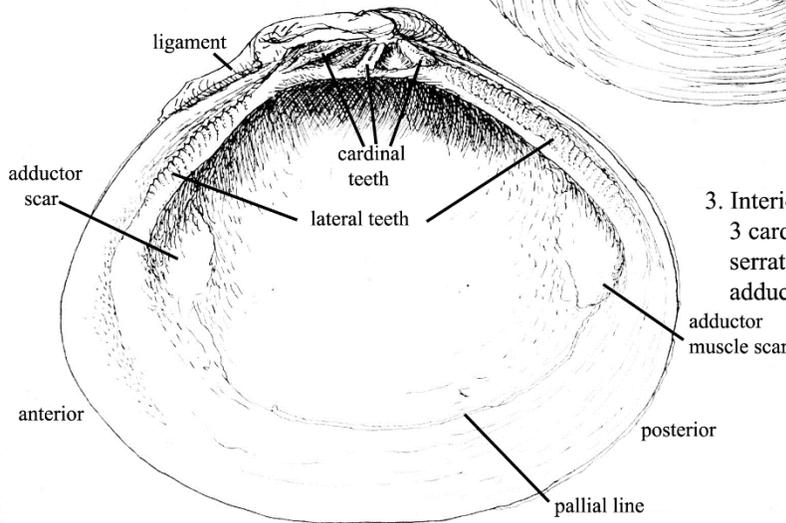
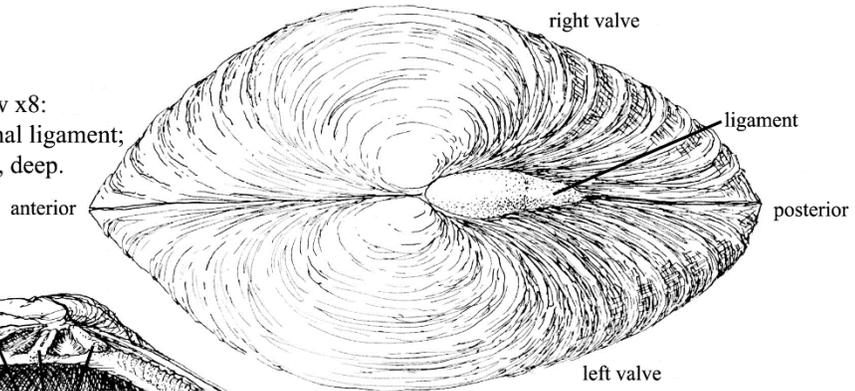
Hinge: The hinge is very elongate, with anterior and posterior serrate lateral teeth (Corbiculidae, Burch 1975) (Fig. 3). There are three hinge teeth on each valve, which are "divergent, pseudocardinals" (Clarke 1981) (Fig. 3). A long row of serrate hinge teeth are present both anteriorly and posteriorly (Fig. 3) (Corbiculidae, Burch 1975). (Note: Ward and Whipple 1963 lists two teeth in each valve, which is a possible error.) The beaks are subcentral (Ward and Whipple 1963), heavy, and inflated (Britton and Morton 1979). The umbones are often

Corbicula fluminea



1. *Corbicula fluminea* (14x12x5.5mm) x8:
left valve; regular, thick, triangular valves;
strong concentric ridges; external ligament
beaks subcentral.

2. Dorsal view x8:
large external ligament;
shell heavy, deep.



3. Interior, left valve:
3 cardinal teeth (each valve); elongate hinge,
serrate lateral teeth; chalky surface; subequal
adductor muscle scars.

eroded, especially in acidic waters (Britton and Morton 1979).

Eyes:

Foot: The foot is rather large (Clarke 1981) (not figured).

Siphons: Siphons are of similar size and shape (Britton and Morton 1979) (not figured).

Burrow:

Possible Misidentifications

The Corbiculidae, of which *Corbicula* is the only North American genus (Burch 1975), are noted for a heavy shell, strong concentric sculpture, a hinge ligament that is internal, and with a peg-shaped chondrophore on the left valve (Coan and Valentich-Scott 2007). *Corbicula fluminea* is characterized by a thick, triangular shell with commarginal ridges and dark brown-black periostracum. There are three other freshwater bivalve families in the Pacific Northwest. The Unionidae are represented by two genera: the monotypic *Gonidea (angulata)* has a smooth but irregular elongate subtriangular shell, with a distinctive high sharp ridge. *Anodonta*, the second genus, has a thin smooth elliptical inflated shell, sometimes winged at the posterior end. It has fine parallel ridges (not deep heavy ones as in Corbiculidae) and its hinges lack teeth. The third family, the Sphaeriidae, belongs to the same superfamily (Sphaeriacea) as the Corbiculidae (Burch 1975). There are several genera, including *Sphaerium*, *Musculium*, and *Pisidium*. Sphaeriidae can have regular valves, subcentral beaks and radial sculpture as do Corbiculidae. The lateral hinge teeth in Sphaeriidae are smooth, however, not serrate as in *Corbicula*.

A great number of species of *Corbicula* have been named worldwide, many of them superfluous. The **taxonomy** of the genus remains unclear, and there is still uncertainty as to how many species have been introduced into North America from Asia and elsewhere (Britton and Morton 1979). It is possible that only *C. fluminea* exists here: M.H. Smith et al. 1979 have suggested, on the basis of electrophoresis, that specimens from 5 major U.S. populations (California, Texas, Arkansas, Tennessee and South Carolina) are all of the same species. There is, however, a great deal of variation in shell

shape, sculpture, etc. Although *C. fluminea* has been synonymized with *C. manilensis*, there are still a few questions about its reproductive habits and longevity (Morton 1979a). *Corbicula fluminalis*, may be larger than *C. fluminea*, could live longer (to 8 years), and seems to occupy river mouths rather than streams (Britton and Morton 1979) (see **taxonomy**).

Ecological Information

Range: Type locality is the Artemovka River in Russia (Kantor et al. 2009) and is endemic to southeast Asia (Morton 1979b). *Corbicula fluminea* is a widespread species with a history of invasion that is well documented; it is a non-native invasive species and, where present, leads to considerable ecological and economic impacts in many aquatic systems (e.g., hydrology, biogeochemistry, biodiversity, Sousa et al. 2008a; Sousa et al. 2008b; Crespo et al. 2015 and references therein). It has been transported (e.g., via ballast water, as bait, etc.; Sousa et al. 2008a) to North America in (first half of 20th century) and South America in the 1960–70s, Europe in the 1980s (see Fig. 1, Crespo et al. 2015). This species was introduced to North America from southeast Asia in the 1930s and is now present in all major U.S. drainages (in the Pacific and Atlantic) below 40° latitude (Britton and Morton 1979; McMahon 1982). Its range in the Pacific Northwest includes Washington, Idaho, Oregon to northern California and it also occurs in the Imperial Valley, California, and in Arizona. There were likely two “epicenters” of human mediated introductions in North America; the first to the northwest from southeast Asia and the second a population in the Ohio River (see Fig. 1, McMahon 1982). On the eastern coast of North America, *C. fluminea* was first observed in Potomac River in 1977 (Cohen et al. 1984; Phelps 1994). Outside of North America, established populations were reported in the Negro River Basin in Patagonia, Argentina, which is the southernmost reach of the species distribution to date worldwide (Molina et al. 2015) and the Iberian Peninsula (Spain and Portugal, Araujo et al. 1993). Potentially high genetic diversity exists within populations, which is observed molecularly (e.g., Hongze Lake, China, Li et al. 1994) and morphologically (a dark morph

observed in southwestern United States, Nichols and Black 1994) (Sousa et al. 2008a).

Local Distribution: Local distribution includes the Columbia River system (from which the illustrated specimen originated), Siuslaw River at Florence, and possibly in the Umpqua River (Carlton 1979).

Habitat: An opportunist, *C. fluminea* can live in quiet or fast moving water, in streams, rivers, canals, lakes and reservoirs. It can utilize either an "r" or a "k" reproductive strategy, and its only limiting factor seems to be space (Britton and Morton 1979). It has expanded geographically very successfully in 50 years, especially into irrigation canals in northern California, where it is considered a pest. In canals, it finds a nursery in the incrustation formed of corophiid amphipod tubes and colonial hydroids on the concrete walls. Locally, the densely packed individuals accumulate as a solid layer (sometimes up to 92 cm thick) composed of clams, fine silt, and mucus. Individuals become so dominant that they have the capacity to change their environment radically. In the Columbia River system, they live in stream bottoms. Prolonged exposure to air can cause death by accumulation of metabolic wastes (rather than desiccation as the clam shell can close tightly). Mean survival is 26.8 days at 20 °C, at high relative humidity (r.h.); 13.9 days at 20 °C., at low r.h.; 8.3 days at 30 °C., at high r.h.; 6.7 days at 30 °C., at low r.h (McMahon 1979). Mortality rate increases with increased turbidity (e.g., 150 nephelometric turbidity units, Avelar et al. 2015). Bioturbation from *C. fluminea* increases soluble and labile phosphorus within sediment (up to 64 mm depths, Chen et al. 2016). Individuals prefer oxygenated, sandy sediment (Crespo et al. 2015). *Corbicula fluminea* is a common bioindicator (e.g., lead contamination, Clarke et al 1979; potassium, Daum et al. 1979; Sousa et al. 2008a) and experiment species (e.g., Baudrimont et al. 1997; Basack et al. 1998; Cataldo et al. 2001; Miller et al. 2005; Vale et al. 2014; Erdogan and Erdogan 2015; Rosa et al. 2015; caffeine, Aguirre-Martinez et al. 2015; Oliveira et al. 2015; metals Bonnail et al. 2016; Oliveria et al. 2016).

Salinity: Considered a freshwater species, but can survive a gradual increase of salinity, i.e., up to salinity of 22 for 80 days. Salinity range reported for *C. fluminea* is 10–14

(Crespo et al. 2015). In shock tests, however, mortality was 50% within 10 days of salinity over 10, and individual sodium uptake was measured 50% sodium at salinity of 4.5 (Evans et al. 1979). The closely related species *C. fluminalis*, is differentiated from *C. fluminea* by some authors as an estuarine, where *C. fluminea* is exclusively freshwater (Araujo et al. et al. 1993 but see Sousa et al. 2008a).

Temperature: Individuals cannot survive cold temperatures (i.e., one severe winter can kill a population, Horning and Keup 1964). Short warm water periods may be a limiting factor in the northern range (Eng 1979). The distribution of this species seems to be limited by low temperatures (Crespo et al. 2015; Gama et al. 2016), as individuals are negatively effected by high temperatures (temperature range 2–34.8 °C, Crespo et al. 2015). Growth occurs only at temperatures over 14 °C, and spawning takes place only at 13–16 °C. (California, Eng 1979).

Tidal Level: Usually a shallow water or near-shore species.

Associates: Individuals become very dominant and outcompete native bivalves within whose communities it can live (Morton 1979a; Crespo et al. 2015). In canals, the amphipod *Corophium spinicorne* provides tubes that harbor recently settled clams; the colonial hydrozoan *Cordylophora lacustris* also provides habitat (Eng 1979). The oligochaete, *Chaetogaster limnaei*, can sometimes be found within the mantle cavity of *C. fluminea* (Eng 1976).

Abundance: Often more than 1,000 individuals per square meter (McMahon 2000; Majdi et al. 2014). Maximum densities in fall, winter, summer were up to 4,500 clams per ~1 square meter in the Delta-Mendota Canal, California (Eng 1979); mean density range was 173–2,990 clams per square meter in a river near Charlottesville, Virginia (Hornback 1992); and up to 525 individuals per square meter in the Negro River Basin (Molina et al. 2015).

Life-History Information

Reproduction: The reproductive organs are composed of an anterior testis and posterior ovary, which both discharge into a common gonoduct (Britton and Morton 1979). (For oocyte and sperm morphology see, Fig. 4

Kraemer and Galloway 1986.) Early reproduction and high fecundity contribute to the success of this species (see **Range**). Both a protogynous and a protandric consecutive hermaphrodite (Britton and Morton 1979), it can also function as a simultaneous hermaphrodite (Crespo et al. 2015), making it highly successful reproductively (Sousa et al. 2008a). Individuals are also capable of androgenetic self-fertilization (Crespo et al. 2015). *Corbicula fluminea* incubates its young for about one month in the inner demibranch of each ctenidium (Morton 1979a) i.e., the branchial water tubes (see Fig. 1, Sousa et al. 2008a). There are two reproductive peaks in California: April to May and August to September and fall and spring peaks were reported in Arkansas, the former lasting longer than the latter in Arkansas (Kraemer and Galloway 1986). (In Kentucky, a cooler climate, there was only but one peak per year.) Cleavage is via a coeloblastula that is 175 µm in diameter at 24 hours post fertilization and development proceeds with cone-shaped gastrulae by 30 hr (175–180 µm); trochophore larvae (180 µm in length); veliger larvae at 24–48 hrs (190–250 µm). **Larva:** Larvae are brooded until they are 210 µm and released as spat with very straight umbo (see Fig. 4, Brink 2001) (see **Reproduction**). Pediveligers develop after 3–5 days (230 µm) at which point the velum is shed metamorphosis occurs into a straight-hinge juvenile (see Fig. 11 and for full description of development see Kraemer and Galloway 1986 and for list of life-history characters, see Table 1, Sousa et al. 2008a). Larvae have a sloping posterior shoulder with rounded posterior end that is slightly shorter than the anterior end. “Larvae” collected in plankton are likely thread drifting (see *Macoma balthica*, *Nutricula tantilla*, *Hiattella arctica*, descriptions in this guide) juveniles that have settled to the benthos and exhibit secondary settlement by riding currents (i.e., not true larvae) (Brink 2001). Larvae are released (as juveniles or late pediveligers, Kraemer and Galloway 1986) into the plankton, and this species is the only freshwater bivalve that does this (Eng 1979; Crespo et al. 2015). Both primary and secondary growth lines give larval shell a “pleated appearance” (Nichols and Black

1994). (For larval identification key for *C. fluminea*, *Driessena polymorpha*, and *D. rosteriformis bugensis* see Nichols and Black 1994).

Juvenile: Like other bivalve species (e.g. *Mytilus edulis*, *Macoma balthica*), post-larval (i.e., juvenile) *C. fluminea* may exploit two dispersal periods. The initial larval dispersal and settlement into the benthos, is followed by potential dispersal from the benthos by thread drifting on water currents via mucous threads by juveniles (i.e., “thread drifting”, Martel and Chia 1991). Clams produce these mucous threads (see Fig. 2, Prezant and Chalermwat 1984) in response to water current stimuli via ctenidial mucocytes (Prezant and Chalermwat 1984). Juvenile settlement flexibility greatly aids in dispersal potential.

Longevity: Two to 4 years (Britton and Morton 1979) or one to 5 years (Sousa et al. 2008a), with large animals in canal bottoms living longest. Two to 3 years were estimated for individuals collected near Charlottesville, Virginia (Hornback 1992).

Growth Rate: Rapid growth is one of the successful strategies of *C. fluminea* (Sousa et al. 2008a). Clams primarily grow from March to October, when temperatures are over 14°C. (Eng 1979). In central California, outside canals, clams grow to a mean of 12 mm the first season, and 15 mm the second (Heinsohn 1958), with two growth rings formed each year (Britton and Morton 1979). Growth varies with depth, with specimens at 8 m deep are longer than those at 12 m (Abbott 1979). Growth of individuals collected in a river near Charlottesville, Virginia was 11.1 mm in the first year, 17.6 mm in the second year (Hornback 1992).

Food: A non-selective filter feeder (Boltovskoy et al. 1995) that also pedal feeds. Diet consists primarily of diatoms (Hanna 1966) and possibly flagellates (i.e., phytoplankton, Foe and Knight 1985). *Corbicula fluminea* removes chlorophyll a from river water with filtration rates that ranged from 13.8–33.9 ml per hour per gram (wet weight) clam (Cohen et al. 1984). Filtration rates measured in three riverine habitats (Tombigbee and Tangipahoa, Mississippi, and Ouachita, Louisiana) ranged from 4–145 ml per hour per gram clam (Way et al. 1990). Increased abundance of *C.*

fluminea reduced abundance of benthic bacteria and flagellates (Hakenkamp et al. 2001; Majdi et al. 2014). However, large populations do not necessarily effect food consumption by competition (Eng 1979).

Predators: Humans use *C. fluminea* for fish bait, and occasionally for food. Other predators include fish (Robinson and Wellborn 1988) and waterfowl (Sinclair and Isom 1963).

Behavior: A burrower and pest in dredged sands that are used to make concrete (Morton 1979a).

Bibliography

1. ABBOTT, T. M. 1979. Asiatic clam (*Corbicula fluminea*) vertical distributions in Dale Hollow Reservoir, Tennessee, p. 111-118. *In*: Proceedings, First International Corbicula Symposium. J. D. Britton (ed.). The Texas Christian University Research Foundation, Fort Worth, Texas.
2. AGUIRRE-MARTINEZ, G. V., A. T. DELVALLS, and M. LAURA MARTINDIAZ. 2015. Yes, caffeine, ibuprofen, carbamazepine, novobiocin and tamoxifen have an effect on *Corbicula fluminea* (Muller, 1774). *Ecotoxicology and Environmental Safety*. 120:142-154.
3. ARAUJO, R., D. MORENO, and M. A. RAMOS. 1993. The Asiatic clam *Corbicula fluminea* (Muller, 1774) (Bivalvia, Corbiculidae) in Europe. *American Malacological Bulletin*. 10:39-49.
4. AVELAR, W. E. P., F. F. NEVES, and M. A. S. LAVRADOR. 2014. Modelling the risk of mortality of *Corbicula fluminea* (Muller, 1774) (Bivalvia: Corbiculidae) exposed to different turbidity conditions. *Brazilian Journal of Biology*. 74:509-514.
5. BASACK, S. B., M. L. ONETO, J. S. FUCHS, E. J. WOOD, and E. M. KESTEN. 1998. Esterases of *Corbicula fluminea* as biomarkers of exposure to organophosphorus pesticides. *Bulletin of Environmental Contamination and Toxicology*. 61:569-576.
6. BAUDRIMONT, M., J. METIVAUD, R. MAURYBRACHET, F. RIBEYRE, and A. BOUDOU. 1997. Bioaccumulation and metallothionein response in the Asiatic clam (*Corbicula fluminea*) after experimental exposure to cadmium and inorganic mercury. *Environmental Toxicology and Chemistry*. 16:2096-2105.
7. BOLTOVSKOY, D., I. IZAGUIRRE, and N. CORREA. 1995. Feeding selectivity of *Corbicula fluminea* (Bivalvia) on natural phytoplankton. *Hydrobiologia*. 312:171-182.
8. BONNAIL, E., A. M. SARMIENTO, T. A. DELVALLS, J. M. NIETO, and I. RIBA. 2016. Assessment of metal contamination, bioavailability, toxicity and bioaccumulation in extreme metallic environments (Iberian Pyrite Belt) using *Corbicula fluminea*. *Science of the Total Environment*. 544:1031-1044.
9. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
10. BRITTON, J. C., and B. MORTON. 1979. *Corbicula* in North America: the evidence reviewed and evaluated, p. 249-287. *In*: Proceedings, First International Corbicula Symposium. J. C. Britton (ed.). Texas Christian University Research Foundation, Fort Worth, Texas.
11. BURCH, J. B. 1975. Freshwater sphaeriacean clams (Mollusca, Pelecypoda) of North America. Malacological Publications, Hamburg, Mich.
12. CATALDO, D., J. C. COLOMBO, D. BOLTOVSKOY, C. BILOS, and P. LANDONI. 2001. Environmental toxicity assessment in the Parana River Delta (Argentina): simultaneous evaluation of selected pollutants and mortality rates of *Corbicula fluminea* (Bivalvia) early juveniles. *Environmental Pollution*. 112:379-389.
13. CHEN, M., S. DING, L. LIU, D. XU, M. GONG, H. TANG, and C. ZHANG. 2016. Kinetics of phosphorus release

- from sediments and its relationship with iron speciation influenced by the mussel (*Corbicula fluminea*) bioturbation. *Science of the Total Environment*. 542:833-840.
14. CLARKE, A. H. 1981. The freshwater molluscs of Canada. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Canada.
 15. CLARKE, J. H. 1979. On the use of *Corbicula fluminea* as indicators of heavy metal contamination, p. 153-163. *In: Proceedings, First International Corbicula Symposium*. J. C. Britton (ed.). Texas Christian University Research Foundation, Fort Worth.
 16. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 17. COHEN, R. R. H., P. V. DRESLER, E. J. P. PHILLIPS, and R. L. CORY. 1984. The Effect of the Asiatic clam, *Corbicula fluminea*, on the phytoplankton of the Potomac River, Maryland. *Limnology and Oceanography*. 29:170-180.
 18. CRESPO, D., M. DOLBETH, S. LESTON, R. SOUSA, and M. A. PARDAL. 2015. Distribution of *Corbicula fluminea* (Muller, 1774) in the invaded range: a geographic approach with notes on species traits variability. *Biological Invasions*. 17:2087-2101.
 19. DAUM, K. A., L. W. NEWLAND, and J. C. HAGEN. 1979. Responses of *Corbicula* to potassium, p. 215-225. *In: Proceedings, First International Corbicula Symposium*. J. C. Britton (ed.). Texas Christian University Research Foundation, Fort Worth.
 20. ENG, L. L. 1976. A note on the occurrence of a symbiotic oligochaete, *Chaetogaster limnaei*, in the mantle cavity of the Asiatic clam, *Corbicula maniliensis*. *Veliger*. 19:208.
 21. —. 1979. Population dynamics of the Asiatic clam, *Corbicula fluminea*, in the concrete lined Delta-Mendota canal of central California, p. 39-68. *In: First International Corbicula Symposium*. J. C. Britton (ed.). Texas Christian University Research Foundation, Fort Worth, Texas.
 22. ERDOGAN, F., and M. ERDOGAN. 2015. Use of the Asian clam (*Corbicula fluminea* Muller, 1774) as a biomechanical filter in ornamental fish culture. *Turkish Journal of Fisheries and Aquatic Sciences*. 15:861-867.
 23. EVANS, L. P. J., C. E. MURPHY, J. C. BRITTON, and L. W. NEWLAND. 1979. Salinity relationships in *Corbicula fluminea* (Müller), p. 193-214. *In: Proceedings, First International Corbicula Symposium*. J. C. Britton (ed.). Texas Christian University Research Foundation, Fort Worth.
 24. FOE, C., and A. KNIGHT. 1985. The effect of phytoplankton and suspended sediment on the growth of *Corbicula fluminea* (Bivalvia). *Hydrobiologia*. 127:105-115.
 25. GAMA, M., D. CRESPO, M. DOLBETH, and P. ANASTACIO. 2016. Predicting global habitat suitability for *Corbicula fluminea* using species distribution models: the importance of different environmental datasets. *Ecological Modelling*. 319:163-169.
 26. HAKENKAMP, C. C., S. G. RIBBLETT, M. A. PALMER, C. M. SWAN, J. W. REID, and M. R. GOODISON. 2001. The impact of an introduced bivalve (*Corbicula fluminea*) on the benthos of a sandy stream. *Freshwater Biology*. 46:491-501.
 27. HANNA, G. D. 1966. Introduced mollusks of western North America. *Occasional Papers of the California Academy of Sciences*. 48:1-108.
 28. HEINSOHN, G. E. 1958. Life history and ecology of the freshwater clam, *Corbicula fluminea*. M.S. University of California, Berkeley, Berkeley, CA.
 29. HORNBACK, D. J. 1992. Life history traits of a riverine population of the Asian clam *Corbicula fluminea*. *American Midland Naturalist*. 127:248-257.

30. HORNING, W. B., and L. KEUP. 1964. Decline of Asiatic clam in Ohio River. *The Nautilus*. 78:29-30.
31. KRAEMER, L. R., and M. GALLOWAR. 1986. Larval development of *Corbicula fluminea*: an appraisal of its heterochrony. *American Malacological Bulletin*. 4:61-79.
32. LI, D., T. ZHANG, S. TANG, L. ZHONG, and X. LIU. 2015. Genetic diversity of wild *Corbicula fluminea* population in the Hongze Lake analyzed by mitochondrial DNA COI gene sequence. *Yuye Kexue Jinzhan*. 36:81-86.
33. MAJDI, N., L. BARDON, and F. GILBERT. 2014. Quantification of sediment reworking by the Asiatic clam *Corbicula fluminea* Muller, 1774. *Hydrobiologia*. 732:85-92.
34. MARTEL, A., and F. S. CHIA. 1991. Drifting and dispersal of small bivalves and gastropods with direct development. *Journal of Experimental Marine Biology and Ecology*. 150:131-147.
35. MCMAHON, R. F. 1979. Tolerance of aerial exposure in the Asiatic clam, *Corbicula fluminea* (Muller), p. 227-241. *In: Proceedings, First International Corbicula Symposium*. J. C. Britton (ed.). Texas Christian University Research Foundation, Fort Worth.
36. —. 1982. The occurrence and spread of the introduced Asiatic freshwater bivalve, *Corbicula fluminea* in North America:1924-1981. *Nautilus*. 96:134-141.
37. —. 2000. Invasive characteristics of the freshwater bivalve *Corbicula fluminea*, p. 315-343. *In: Nonindigenous freshwater organisms: vectors, biology and impacts*. R. Claudi and J. Leach (eds.). Lewis Publishers, Boca Raton.
38. MILLER, W. A., E. R. ATWILL, I. A. GARDNER, M. A. MILLER, H. M. FRITZ, R. P. HEDRICK, A. C. MELLI, N. M. BARNES, and P. A. CONRAD. 2005. Clams (*Corbicula fluminea*) as bioindicators of fecal contamination with *Cryptosporidium* and *Giardia* spp. in freshwater ecosystems in California. *International Journal for Parasitology*. 35:673-684.
39. MOLINA, L. M., P. J. PEREYRA, N. G. MOLINA CARRIZO, and M. A. ABRAMETO. 2015. Here come the clam: southernmost record worldwide of the Asian clam *Corbicula fluminea* (Patagonia, Argentina). *Rosiskii Zhurnal Biologicheskikh Invazii*. 1:96-102.
40. MORTON, B. 1977a. *Corbicula* in Asia, p. 15-38. *In: Proceedings of the First International Corbicula Symposium*. J. C. Britton (ed.). Texas Christian University Research Foundation, Fort Worth, TX.
41. —. 1977b. Population dynamics of *Corbicula fluminea* (Bivalvia, Corbiculacea) in Plover Cove Reservoir, Hong Kong. *Journal of Zoology*. 181:21-42.
42. —. 1979. Freshwater fouling bivalves, p. 1-14. *In: Proceedings, First International Corbicula Symposium*. J. C. Britton (ed.). Texas Christian University Research Foundation, Fort Worth.
43. NICHOLS, S. J., and M. G. BLACK. 1994. Identification of larvae: the Zebra Mussel (*Dreissena polymorpha*), Quagga Mussel (*Dreissena rostriformis Bugensis*), and Asian Clam (*Corbicula fluminea*). *Canadian Journal of Zoology*. 72:406-417.
44. OLIVEIRA, C., P. VILARES, and L. GUILHERRNINO. 2015a. Integrated biomarker responses of the invasive species *Corbicula fluminea* in relation to environmental abiotic conditions: A potential indicator of the likelihood of clam's summer mortality syndrome. *Comparative Biochemistry and Physiology: A-Molecular and Integrative Physiology*. 182:27-37.
45. OLIVEIRA, P., M. LOPES-LIMA, J. MACHADO, and L. GUILHERMINO. 2015b. Comparative sensitivity of European native (*Anodonta anatina*) and exotic (*Corbicula fluminea*) bivalves to mercury. *Estuarine Coastal and Shelf Science*. 167:191-198.

46. PHELPS, H. L. 1994. The Asiatic Clam (*Corbicula fluminea*) invasion and system-level ecological change in the Potomac River Estuary near Washington, D.C.T. *Estuaries*. 17:614-621.
47. PRASHAD, B. 1929. Revision of the Asiatic species of the genus *Corbicula*. III. The species of the genus *Corbicula* from China, southeastern Russia, Tibet, Formosa, and the Philippine Islands. *Memoirs of the Indian Museum*. 9:49-72.
48. PREZANT, R. S., and K. CHALERMWAT. 1984. Flotation of the bivalve *Corbicula fluminea* as a means of dispersal. *Science*. 225:1491-1493.
49. ROBINSON, J. V., and G. A. WELLBORN. 1988. Ecological resistance to the invasion of a freshwater clam, *Corbicula fluminea*: fish predation effects. *Oecologia*. 77:445-452.
50. ROSA, I. C., R. GARRIDO, A. RE, J. GOMES, J. L. PEREIRA, F. GONCALVES, and R. COSTA. 2015. Sensitivity of the invasive bivalve *Corbicula fluminea* to candidate control chemicals: the role of dissolved oxygen conditions. *Science of the Total Environment*. 536:825-830.
51. SINCLAIR, R. M., and B. G. ISOM. 1963. Further studies on the introduced Asiatic clam (*Corbicula*) in Tennessee. Tennessee Department of Public Health, Nashville.
52. SMITH, M. H., J. C. BRITTON, P. BURKE, R. K. CHESSER, W. M. SMITH, and J. HAGEN. 1979. Genetic variability in *Corbicula*, an invading species, p. 243-248. *In: Proceedings, First International Corbicula Symposium*. J. C. Britton (ed.). Texas Christian University Research Foundation, Fort Worth.
53. SOUSA, R., C. ANTUNES, and L. GUILHERMINO. 2008a. Ecology of the invasive Asian clam *Corbicula fluminea* (Muller, 1774) in aquatic ecosystems: an overview. *Annales De Limnologie-International Journal of Limnology*. 44:85-94.
54. SOUSA, R., A. J. A. NOGUEIRA, M. B. GASPAS, C. ANTUNES, and L. GUILHERMINO. 2008b. Growth and extremely high production of the non-indigenous invasive species *Corbicula fluminea* (Muller, 1774): possible implications for ecosystem functioning. *Estuarine Coastal and Shelf Science*. 80:289-295.
55. VALE, G., C. FRANCO, M. S. DINIZ, M. M. C. DOS SANTOS, and R. F. DOMINGOS. 2014. Bioavailability of cadmium and biochemical responses on the freshwater bivalve *Corbicula fluminea*: the role of TiO₂ nanoparticles. *Ecotoxicology and Environmental Safety*. 109:161-168.
56. WARD, H. B., and G. C. WHIPPLE. 1963. *Freshwater biology*, New York.
57. WAY, C. M., D. J. HORNBAUGH, C. A. MILLERWAY, B. S. PAYNE, and A. C. MILLER. 1990. Dynamics of filter feeding in *Corbicula fluminea* (Bivalvia, Corbiculidae). *Canadian Journal of Zoology*. 68:115-120.

Updated 2016

Tresus capax

The gaper clam, horseneck clam, or fat gaper

Phylum: Mollusca
Class: Bivalvia, Heterodonta
Order: Veneroida
Family: Mactridae

Taxonomy: Originally described as *Lutraria capax* (in 1850 by Gould), few synonyms are known and are rarely used (e.g., *L. maxima* and *Schizothaerus capax*).

Description

Size: Individuals up to 20 cm in length, with average size 10–12 cm. *Tresus capax* are some of the largest northwest clams (Kozloff 1993), some specimens weigh up to 1.8 kg (Ricketts and Calvin 1971).

Color: Shell chalky white and occasionally with patches of black due to the presence of sulfides (Kozloff 1993). The periostracum is dull brown in color, and often flaking.

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). The Veneroida is a large and diverse bivalve heterodont order that is characterized by well-developed hinge teeth. There are 22 local families, and members of the family Mactridae are characterized by a A-shaped cardinal tooth (see Plate 396F, Coan and Valentich-Scott 2007; Fig. 2a).

Body: (Fig. 295, Kozloff 1993).

Color:

Interior: Biphasic action of the heart is facilitated by acetylcholine in *Mytilus planulatus*, *M. edulis*, *Spisula solidissima*, and *T. capax* (Greenberg 1970). Stomach described as Type V (for definition, see Reid 1977). A visceral “skirt”, or a fold along the edge of the mantle tissue, often gives a home to commensal pea crabs in the genus *Pinnixa*. Maximal systolic pressure was recorded for *T. capax* to be 13 cm H₂O, which is higher than the 11 cm H₂O recorded for *Saxidomus giganteus* (Florey and Cahill 1977) (see description in this guide).

Exterior:

Byssus:

Gills:

Shell: Overall shell shape is oval, with larger specimens quadrate (Fig. 1). The posterior end

is truncate, and gapes widely (Figs. 1–2). Individuals 1.5 times long as tall (Kozloff 1993).

Interior: Porcelaneous and white, with two adductor muscle scars of similar shape, and a long pallial sinus (Fig. 2).

Exterior: Right and left valves are similar and with smooth sculpture, with only concentric rings. Some periostracum, but not necessarily covering the entire shell. Beaks are one third from anterior end.

Hinge: One small cardinal tooth on each valve, and a J-shaped, socket-like chondrophore (Fig. 2). The left valve is with A-shaped tooth (Fig. 2a).

Eyes:

Foot:

Siphons: Large, fused siphons are retractable (almost completely), and with rather leathery tips, and small, inconspicuous, leathery plates at the tip (Kozloff 1993).

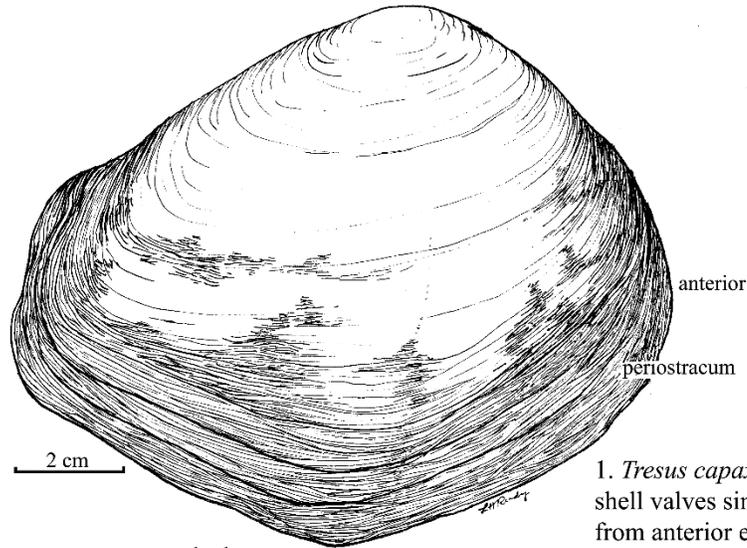
Burrow: Burrow depth ranges from 30–50 cm and depends on substrate type (e.g., those in stiff clay have more shallow burrows than those in soft mud) (Kozloff 1993).

Tresus capax individuals apparently lose the ability to re-burrow themselves once they reach 60–75 mm in length (Pohlo 1964 in Zhang and Campbell 2002).

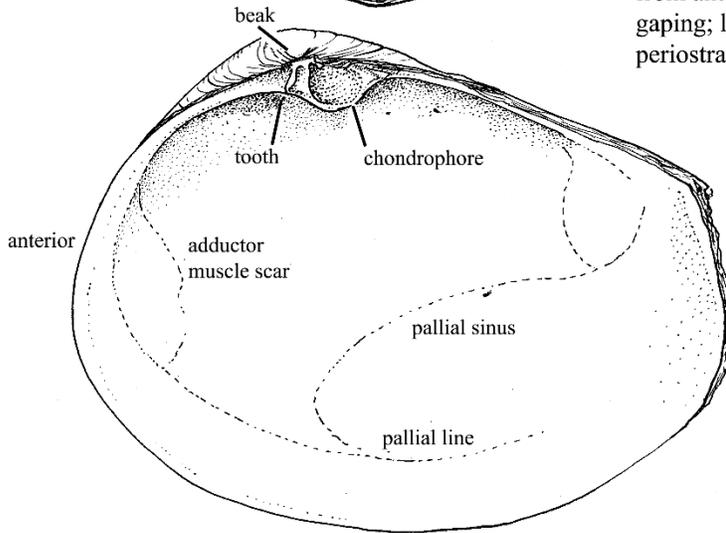
Possible Misidentifications

The bivalve family Mactridae is monophyletic based on both molecular and morphological characters and appears in the fossil record beginning in the Cretaceous (Rice and Roddick 1993); there are seven species reported locally. This heterodont family is characterized by an internal ligament, large shells (greater than 25 mm in length) that are internally porcelaneous and a pallial line with conspicuous sinus (Coan and Valentich-Scott 2007). The anterior cardinal tooth on the left valve has an inverted A-shape in mactrids (see Fig. 2a), unlike the family Semelidae. Only those in the genus *Tresus* have a shell with a conspicuous gape posteriorly (Fig. 3). In *T. nuttallii*, the shells

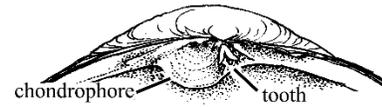
Tresus capax



1. *Tresus capax*, exterior, right valve x1: shell valves similar, oval-quadrate; beaks 1/3 from anterior end; posterior end truncate, gaping; large, fused, leathery siphons; some periostracum.

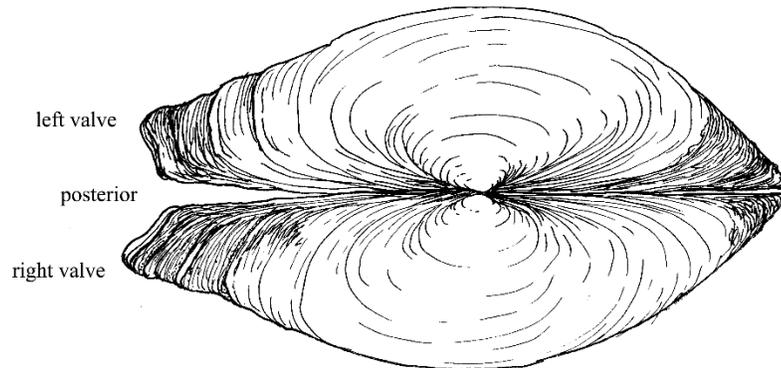


2. Interior, right valve: muscle scars similar; deep pallial sinus; small, J-shaped tooth; socket-like chondrophore containing ligament.



2a. Hinge area, left valve: chondrophore and A-shaped tooth.

3. (Dorsal view).



are ovate or elongate with a posterior end that is longer than the anterior. Sometimes called the southern or Pacific gaper clam, *Tresus nuttallii* occasionally occurs in our area, but is common only from Tomales Bay, California south. It is more elongate than *T. capax*, and has prominent horny plates on its siphon, not just leathery tips. Its periostracum is more extensive and its beaks closer to the anterior end than those of *T. capax*. The shell of *T. capax* the shell is ovate to rhomboidal in shape (Coan and Valentich-Scott 2007). *Tresus nuttallii* also lacks the visceral "skirt" of mantle tissue found in *T. capax* (Coan and Valentich-Scott 2007). This skirt is an elongated inner lamellar palp that hangs dorsally and covers a portion of the posterior visceral mass. *Tresus capax* also hosts up to three species of pea crabs (see **Associates**), which are not found in *T. nuttallii*. Young individuals of both *Tresus* species can be easily confused with *Mya arenaria*, the softshell clam. *Mya arenaria*, however, has a chondrophore on only one valve, its posterior is rounded, not truncate and its siphons lack the leather-like flaps found in *Tresus* local species. *Tresus allomyax*, an offshore species, is also reported from central California to Oregon (Coan and Valentich-Scott 2007).

All other mactrid species have shells with a narrowly gaping or completely closed posterior (Coan and Valentich-Scott 2007). *Mactromeris* species have a chondrophore that projects ventrally. *Mactromeris catilliformis* has a shorter anterior end than posterior, and the opposite is true for *M. hemphillii*. *Mactromeris californica* and *Simomactra* species lack a chondrophore and only members of the latter genus have a beak without undulations. In *S. planulata*, the shell valves are subequilateral however the shell in *S. falcata* is longer anteriorly.

Ecological Information

Range: Type locality is Puget Sound, Washington (Orr et al. 2013). Known eastern Pacific range from Kodiak, Alaska, to San Francisco. Populations uncommon south of Humboldt Bay, where the congener *Tresus nuttallii* becomes the more common species (Coan and Valentich-Scott 2007).

Local Distribution: Local distribution in many of Oregon's larger estuaries (e.g., Coos,

Netarts, Tillamook, Yaquina). However, this species is not yet found in Siletz, or Nestucca, which is potentially due to the stronger currents in the latter estuaries.

Habitat: Occurs in sheltered intertidal flats, e.g., in sand, mud, mud with gravel and shell hash. Individuals also occur in stiff clay down to 30 cm. Occurs in eelgrass (e.g., *Zostera marina*) beds, where digging for their harvest (see **Predators**) does not seem to effect eelgrass production (Yaquina Bay, Oregon, Boese 2002), as well as non-native seaweed species (e.g., *Sargassum muticum*, White and Orr 2011). However, they are rarely found within mudflats dominated by ghost shrimp, *N. californiensis* (see description in this guide), presumably because of the unstable substrate these create (Hancock 1979). *Tresus capax* is occasionally used as a bioindicator species in toxicity testing (e.g., tributyltin, Horiguchi et al. 2003).

Salinity:

Temperature: A temperate northwest species, where temperatures range 9–15° (Matchell et al. 1971).

Tidal Level: Occurs from 25–60 cm below the surface and mid- to subtidal to 50-meter depths (Zhang and Campbell 2002).

Associates: Hosts at least three pea crab species within the mantle cavity (Pearce 1965; Campos-Gonzalez 1986) including *Pinnixa faba* (see Fig. 296, Kozloff 1993; description in this guide), *P. littoralis*, *Fabia subquadrata* (Kozloff 1993). They ingest material (e.g., diatoms) brought in by the clam and their presence make the mantle tissue irritated or blistered (Kozloff 1993). Only one adult pair is found per clam, however, several juveniles can be present (Kozloff 1993). Occasionally inhabited by nemertean worm *Malacobdella grossa* (Haderlie 1980). Coexists with the congener, *T. nuttallii*, in Humboldt Bay and occasionally in Oregon and Washington and British Columbia, Canada (Zhang and Campbell 2002). However, *T. capax* is much more commonly found (Kozloff 1993).

Abundance: Very abundant and commonly dug in local estuaries. Constituted nearly all of Coos Bay's commercial clam catch, and up to 60% of Oregon's total commercial catch (Hancock et al. 1979). Individuals can be found at densities of over 108 individuals/m² (Yaquina

Bay, Hancock et al. 1979). However, *T. capax* is less common south of Humboldt Bay (see **Range**); high mean densities of 24.8 individuals/m² were reported for populations in Humboldt Bay, California (Wendell 1976). Individuals more abundant in shallow than deeper water (Campbell and Bourne 2000).

Life-History Information

Reproduction: Dioecious. Individuals free-spawn in Jan–March (northern California, Oregon, Washington) and mid February–May (Strait of Georgia, Bourne and Smith 1972b; Brusa et al. 1978; Kabat and O’Foighil 1987). In Humboldt Bay, California, gametes were most abundant from August to October, when water temperatures were high, and spawning coincides with a drop in water temperatures (January to March) and salinity; sex ratios were approximately 1:1 (Machell and De Martini 1971). Spawning in late winter with peaks in March to April have also been reported for Yaquina Bay, Oregon and the periodicity may be influenced by lunar cycles (Hancock et al. 1979; Breed-Willeke and Hancock 1980). Oocytes are 60–70 µm in diameter and sperm heads 3.2 µm in length with tails 30 µm long. Development proceeds as follows at 13°C (Kabat and O’Foighil 1987; Bourne and Smith 1972a, 1972b): first polar body at 40 min, first cleavage at 90 min, trochophore larva at 24 hr, and straight hinge veligers at 48 hrs (Kabat and O’Foighil 1987).

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the “D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone (see Fig. 1, Caddy 1969). Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is

called a pediveliger (see Fig. 1, Caddy 1969; Kabat and O’Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001). The straight-hinge veliger larvae of *T. capax* are 75–80 x 60 µm, when umbones are present they are 140–150 µm, pediveligers are 230–250 µm and at settlement individuals are 250 x 240 µm. Straight hinge veligers have an anterior end that is longer and more pointed than the posterior (see Fig. 4, Brink 2001) and the bottom half of the anterior end slopes dramatically ventrally (Brink 2001). Eventually, the umbo becomes more angled, the posterior end becomes blunt, and the anterior end pointed. The anterior shoulder is longer than the posterior and metamorphosis occurs when individuals are 260–280 µm (Bourne and Smith 1972a; Brink 2001), after 34 days (5°C), 26 days (10°C), or 24 days (15°C) (Bourne and Smith 1972a; Kabat and O’Foighil 1987). Larvae do not develop at temperatures of 20°C and higher (Bourne and Smith 1972a). Larval recruitment was variable from 1969–1973 throughout 16 sites in Humboldt Bay, California (from 6.7 to 100 recruits/0.25 m², see Wendell 1976).

Juvenile: Sexual maturity is reached after 3–4 years, when individuals are at least 70 mm in length (Bourne and Smith 1972b; Kabat and O’Foighil 1987).

Longevity: Four to 29 years (Tofino, British Columbia, Canada, Campbell et al. 2009). The best aging technique is counting the annuli (see **Growth**) on chondrophore (Hancock et al. 1979). Individuals that are commercially and recreationally harvested are approximately five years old (Hancock et al. 1979). The mean age of individuals collected from Ritchie Bay in southern British Columbia, Canada were 10.8 years old (and 148 mm in length Campbell and Bourne 2000). Wendell (1976) estimated the longevity to be 15–20 years in *T. capax* populations from Humboldt Bay, California (Wendell 1976).

Growth Rate: Subtidal individuals that are over four years old are larger and grow faster than intertidal specimens (Hancock 1979; Breed-Willeke and Hancock 1980); growth rates from low intertidal and subtidal zones were greater than those for intertidal zones in southern British Columbia, Canada (Campbell and Bourne 2000). Most growth occurs in late spring and summer when planktonic food is most plentiful. Individuals then store fat

and glycogen throughout the remainder of the year (Kozloff 1974). Individuals are 110 mm in length when 15–16 years old (Kabat and O’Foighil 1987). Growth rates are estimated by counting growth zones on the chondrophore, as shell growth alternates between narrow conchoilin (transparent) and wide aragonite (opaque) zones (Gaumer 1977; Campbell et al. 2009). Growth rates measured at two locations in southern British Columbia, Canada were 98 and 84 mm at 5 years, 132 and 123 mm at 10 years, and 149 and 145 mm at 15 yrs in Seal and Doyle Islands, respectively (Bourne and Smith 1972b).

Food: A suspension feeder (Reid 1977) that eats planktonic organisms and detritus particles. Interestingly, *Saxidomus* spp. (*S. giganteus*, *S. nuttallii*) are more resistant to toxic (saxitoxin) dinoflagellates than other co-occurring bivalves, like *T. capax* (Kvitek and Beitler 1991).

Predators: Known predators include birds (e.g., glaucous-winged gull, Kvitek 1991), human harvest (e.g., Cannon and Burchell 2009), the snail *Polinices*, crab (*Cancer magister*), and sea stars in the genus *Pisaster*. Haplosporidian parasitic infestation was recorded in 89% of clams from Oregon estuaries (Gaumer 1977). Occasionally sea otters, but *T. capax* likely avoids otter predation in its deep burrow (Kvitek and Oliver 1992; Kvitek et al. 1992). As larvae, *T. capax* veligers are preyed upon by planktonic predators and suspension feeders. A commercial fishery was developed in British Columbia, Canada (Zhang and Campbell 2002), and the fishery in Coos Bay produced over 25,166 kg (Gaumer 1977).

Behavior: A weak burrower, *T. capax* individuals can still be found rather deep (e.g., 50 cm, see **Burrow**) in the substrate.

Bibliography

- BOESE, B. L. 2002. Effects of recreational clam harvesting on eelgrass (*Zostera marina*) and associated infaunal invertebrates: in situ manipulative experiments. *Aquatic Botany*. 73:63-74.
- BOURNE, N., and D. W. SMITH. 1972a. Breeding and growth of the horse clam, *Tresus capax* (Gould), in southern British Columbia. *Proceedings of the National Shellfisheries Association*. 62:38-46.
- . 1972b. The effect of temperature on the larval development of the horse clam, *Tresus capax* (Gould). *Proceedings of the National Shellfisheries Association*. 62:35-37.
- BREED-WILLEKE, G. M., and D. R. HANCOCK. 1980. Growth and reproduction of subtidal and intertidal populations of the gaper clam, *Tresus capax*, from Yaquina Bay, Oregon, USA. *Proceedings National Shellfisheries Association*. 70:1-13.
- BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
- BRUSCA, G. J., and R. C. BRUSCA. 1978. *A naturalist's seashore guide*. Mad River Press, Arcata, CA.
- CAMPBELL, A., and N. BOURNE. 2000. Population biology of gaper (horse) clams, *Tresus capax* and *T. nuttallii*, in southern British Columbia, Canada. *Journal of Shellfish Research*. 19:933-942.
- CAMPBELL, B. N., J. B. GROOT, and S. M. MAHANNAH. 2009. An investigation into ageing methods for horse clams (*Tresus nuttallii* and *T. capax*). *Canadian Technical Report of Fisheries and Aquatic Sciences*. 2765:1-25.
- CANNON, A., and M. BURCHELL. 2009. Clam growth-stage profiles as a measure of harvest intensity and resource management on the central coast of British Columbia. *Journal of Archaeological Science*. 36:1050-1060.
- COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
- FLOREY, E., and M. A. CAHILL. 1977. Hemodynamics in Lamellibranch mollusks: confirmation of constant-volume mechanism of auricular and

- ventricular filling. Remarks on heart as site of ultrafiltration. *Comparative Biochemistry and Physiology. A-Physiology*. 57:47-52.
12. GAUMER, T. F. 1977. Recent clam studies in Oregon's estuaries. *Proceedings National Shellfisheries Association*. 67:126-127.
 13. GREENBER, M. J. 1970. A comparison of acetylcholine structure/activity relations on hearts of bivalve molluscs. *Comparative Biochemistry and Physiology*. 33:259-294.
 14. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 15. HANCOCK, D. R., T. F. GAUMER, G. B. WILLEKE, G. P. ROBART, and J. FLYNN. 1979. Subtidal clam populations: distribution, abundance, and ecology. Oregon State University, Sea Grant College Program, Corvallis.
 16. HORIGUCHI, T., Z. LI, S. UNO, M. SHIMIZU, H. SHIRAISHI, M. MORITA, J. A. J. THOMPSON, and C. D. LEVINGS. 2004. Contamination of organotin compounds and imposex in molluscs from Vancouver, Canada. *Marine Environmental Research*. 57:75-88.
 17. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 18. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 19. KVITEK, R. G. 1991. Sequestered paralytic shellfish poisoning toxins mediate glaucous-winged gull predation on bivalve prey. *Auk*. 108:381-392.
 20. KVITEK, R. G., and M. K. BEITLER. 1991. Relative insensitivity of butter clam neurons to saxitoxin: a pre-adaptation for sequestering paralytic shellfish poisoning toxins as a chemical defense. *Marine Ecology Progress Series*. 69:47-54.
 21. KVITEK, R. G., and J. S. OLIVER. 1992. Influence of sea otters on soft-bottom prey communities in southeast Alaska. *Marine Ecology Progress Series*. 82:103-113.
 22. KVITEK, R. G., J. S. OLIVER, A. R. DEGANGE, and B. S. ANDERSON. 1992. Changes in Alaskan soft bottom prey communities along a gradient in sea otter predation. *Ecology*. 73:413-428.
 23. MACHELL, J. R., and J. D. DEMARTINI. 1971. An annual reproductive cycle of the gaper clam, *Tresus capax* (Gould) in South Humboldt Bay, California. *California Fish and Game*. 57:274-282.
 24. ORR, J. W., D. T. DRUMM, R. VAN SYOC, K. P. MASLENIKOV, T. W. PIETSCH, D. E. STEVENSON, and R. R. LAUTH. 2013. An annotated checklist of bottom-trawled macroinvertebrates of Alaska, with an evaluation of identifications in the Alaska Fisheries Science Center Bottom-Trawl Survey Database. NPRB Project 1016 Final Report. North Pacific Research Board, Alaska.
 25. PEARCE, J. B. On the distribution of *Tresus nuttalli* and *Tresus capax* (Pelecypoda:Mactridae) in the waters of Puget Sound and the San Juan Archipelago. *The Veliger*. 7:166-170.
 26. REID, R. G. B. 1978. The systematic adaptive and physiological significance of proteolytic enzyme distribution in bivalves. *Veliger*. 20:260-265.
 27. RICE, E. L., D. RODDICK, and R. K. SINGH. 1993. A comparison of molluscan (Bivalvia) phylogenies based on palaeontological and molecular data. *Molecular Marine Biology and Biotechnology*. 2:137-146.
 28. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an

- account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
29. —. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 30. SWAN, E. F., and J. H. FINUCANE. 1952. Observations on the genus *Schizothaerus*. *Nautilus*. 66:19-26.
 31. WENDELL, F., J. D. DEMARTINI, P. DINNEI, and J. SIECKE. 1976. The ecology of the gaper or horse clam, *Tresus capax* (Gould 1850) (Bivalvia, Mactridae), in Humboldt Bay, California. *California Fish and Game*. 62:41-64.
 32. WHITE, L. F., and L. C. ORR. 2011. Native clams facilitate invasive species in an eelgrass bed. *Marine Ecology Progress Series*. 424:87-95.
 33. ZHANG, Z., and A. CAMPBELL. 2002. Application of a stochastic spawning stock biomass per recruit model for the horse clam fishery in British Columbia. *Fisheries Research*. 57:9-23.

Updated 2016

Siliqua patula

The flat razor clam

Phylum: Mollusca
Class: Bivalvia; Heterodonta
Order: Veneroida
Family: Pharidae

Taxonomy: The familial designation of this species has changed frequently over time. Previously in the Solenidae, current intertidal guides include *S. patula* in the Pharidae (e.g., Coan and Valentich-Scott 2007). The superfamily Solenacea includes infaunal soft bottom dwelling bivalves and contains the two families: Solenidae and Pharidae (= Cultellidae, von Cosel 1993) (Remacha-Trivino and Anadon 2006). In 1788, Dixon described *S. patula* from specimens collected in Alaska (see **Range**) and Conrad described the same species, under the name *Solen nuttallii* from specimens collected in the Columbia River in 1838 (Weymouth et al. 1926). These names were later synonymized, thus known synonyms for *Siliqua patula* include *Solen nuttallii*, *Solecurtus nuttallii*. Occasionally, researchers also indicate a subspecific epithet (e.g., *Siliqua siliqua patula*) or variations (e.g., *Siliqua patula* var. *nuttallii*, based on rib morphology, see **Possible Misidentifications**) (Oldroyd 1924).

Description

Size: Individuals up to 190 mm (Haderlie and Abbott 1980; Coan and Valentich-Scott 2007), with average size adults over 40 mm (Coan and Carlton 1975).

Color: Periostracum is smooth, brown, shiny, and lacquer-like (Ricketts and Calvin 1952). The shell exterior is white, obscurely rayed, with faint violet coloration and the interior is also white, but tinged with violet and pink (Haderlie and Abbott 1980).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Solenid and pharid bivalves are burrowers and some species are quite fast (e.g., *Siliqua patula*, see description in this guide). They have shells that are longer than wide and often razor-like at the opening edge (see Plate 397G, Coan and Valentich-Scott 2007).

Body: (see Plate 29 Ricketts and Calvin 1952; Fig 259 Kozloff 1993).

Color:

Interior: (see Fig 5, Pohlo 1963).

Exterior:

Byssus:

Gills:

Shell: The shell in *S. patula* is thin and with sharp (i.e., razor-like) edges and a thin profile (Fig. 4). Thin, long, fragile shell (Ricketts and Calvin 1952), with gapes at both ends (Haderlie and Abbott 1980). Shell smooth inside and out (Dixon 1789), elongate, rather cylindrical and the length is about 2.5 times the width.

Interior: Prominent internal vertical rib extending from beak to margin (Haderlie and Abbott 1980).

Exterior: Both valves are similar and gape at both ends. The beaks are subcentral and toward anterior end, and the posterior end is round.

Hinge: The hinge ligament is completely external, and not seated on a nymph (Fig. 2). The left valve is with four cardinal teeth, while the right valve is with two (Fig. 2). A vertical or radial rib projects downward and anteriorly from hinge in both valves (*Siliqua*, Keen and Coan 1974) (Fig. 2).

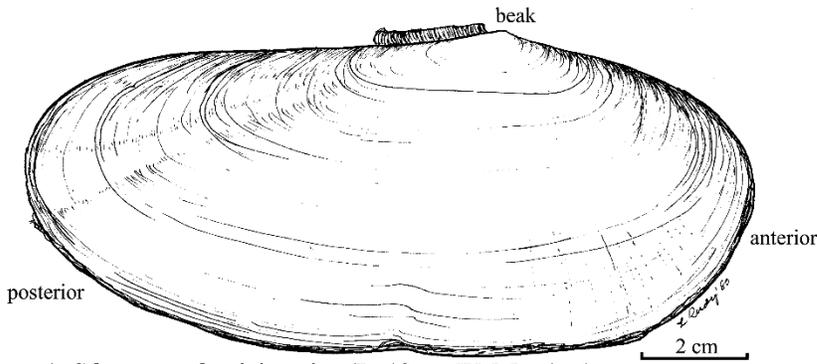
Eyes:

Foot: The foot in *S. patula* projects to a length that is one half the total shell length and has a muscular flap (Haderlie and Abbott 1980). It aids in digging by anchoring within the sediment and contracting such that the body is pulled downward (Ricketts and Calvin 1952) (see **Burrow** and **Behavior**).

Siphons: Siphons are short and fused at the tips, except at the very end (Haderlie and Abbott 1980) (Fig. 4). The exhalant and inhalant openings are ringed by tentacles.

Burrow: A fast burrower, *S. patula* uses its **foot** to anchor and muscular contractions to pull body downward. Individuals can completely bury itself within seven seconds (Ricketts and Calvin 1952) and the burrowing

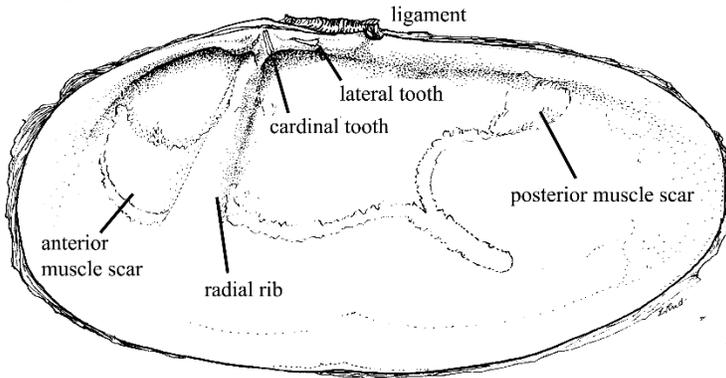
Siliqua patula



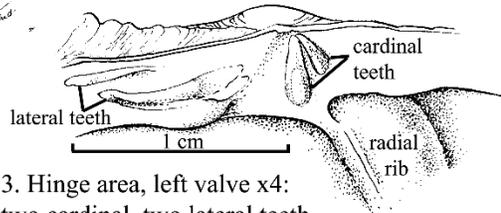
1. *Siliqua patula*, right valve (L: 13cm, W:5.5cm) x1:
length 2.5x width; shell cylindrical, shiny, brown; beaks subcentral,
slightly anterior; posterior rounded.



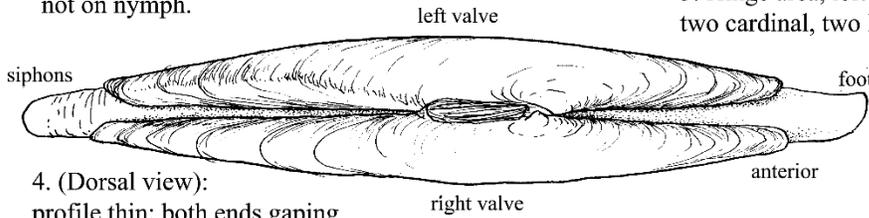
1a. *Malacobdella grossa* x2:
actual size 2.5 cm, commensal
nemertean (Smith & Carlton, 1975).



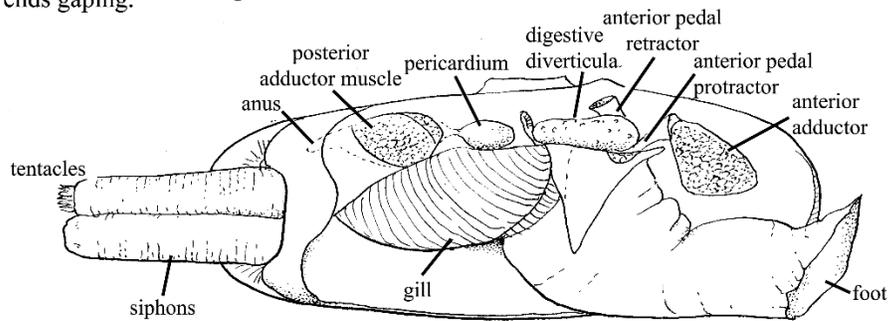
2. Interior, right valve:
one cardinal tooth, one lateral tooth;
prominent radial rib; ligament external,
not on nymph.



3. Hinge area, left valve x4:
two cardinal, two lateral teeth.



4. (Dorsal view):
profile thin; both ends gaping.



5. Dissection, right valve removed
(Pohlo, 1963).

speed allows them to avoid the reach of many clam diggers. Burrowing behavior leaves a slight dimple in the sand at the surface (not unlike a thumb imprint). There is no permanent burrow, unlike the similar species *Solen sicarius* (see description in this guide) (Haderlie and Abbott 1980). Individuals orient vertically within the sediment (see Fig 3, Pohlo 1963; Haderlie and Abbott 1980).

Possible Misidentifications

Solenidae and Pharidae are two razor clam families represented locally and pharid genera were recently placed in the former family (see previous editions of this guide). They are both characterized by cylindrical shells that are about 2.5 times as long as high and gape at both ends. They have no dorsal margin ears (compare to Pectinidae, see Plate 394E, Coan and Valentich-Scott 2007), a hinge with ligament that is entirely external and dorsal, equally shaped adductor muscle scars (compare to *Mytilus trossulus*, this guide), and shells that do not have prominent radial sculpturing (Coan and Valentich-Scott 2007). The difference between the two families is that members of the Pharidae have one shell valve with two cardinal teeth and the other with four, while the Solenidae have a single cardinal tooth on each shell valve (Coan and Valentich-Scott 2007). Other local razor-shaped clams besides the Solenidae such as the Mytilidae include some genera (e.g. *Adula*) which are also long and cylindrical. *Adula* (see *A. californiensis*, this guide) are usually a boring species, however, having hairy posterodorsal slopes, a very small anterior adductor scar, and no hinge teeth (Coan and Valentich-Scott 2007). Hiattellidae, including the geoduck, *Panopea generosa* have large, quadrate, gaping bivalves, without hinge teeth, and with nearly equal adductor muscle scars (Keen and Coan 1974).

Four species are reported locally in the Pharidae. *Siliqua patula* has an internal rib that slopes anteriorly, a wide and tapering posterior end. *Siliqua lucida* is smaller than *S. patula* (< 55 mm in length) and has an internal rib that is vertical and narrow and a posterior end that is truncate. It has been suggested that *S. lucida* are simply young *S. patula* individuals (Hertlein 1961), but this is not yet known. *Siliqua lucida* lives in protected bay sands and has concentric

brown bands on its exterior. Although variations in *S. patula* have been synonymized, occasionally readers will find references to *S. patula* var. *nuttallii*, which is more oval shape, with purple beaks and four hinge teeth in the left valve, not two (Oldroyd 1924). *Ensis myrae* and *Siliqua alba* are offshore species and *E. myrae* has a shell that is long and thin.

Only two species, in the genus *Solen*, are reported locally in the Solenidae, they have an almost straight dorsal margin, a terminal beak, and one cardinal tooth in each valve (Keen 1971). *Solen rostiformis* (= *S. rosaceus*, but see Pohlo 1963; von Cosel 1992) has a thin shell that tapers and a periostracum that is lighter than *S. sicarius*; it is light olive green to brown in color. *Solen rostiformis* is a pink shelled clam and its siphons are annulated (and it can regenerate them when disturbed, Pohlo 1963). It lives in sandier situations than does *S. sicarius* (Coan and Carlton 1975). *Solen sicarius*, on the other hand, has a thick shell, a blunt posterior ('the blunt razor shell') and a dark brown periostracum. *Solen sicarius* is found occasionally in permanent burrows in mud or muddy sand (Kozloff 1974) and is the species most likely to be confused with *Siliqua patula*. It lacks an interior vertical rib and multiple hinge teeth, and is four times as long as wide, not 2.5 times, as in *S. patula* (Keen and Coan 1974). Furthermore, the profile in *S. patula* is much more oval, and not as cylindrical as in *Solen sicarius*.

One long, cylindrical bivalve of the family Solecurtidae, *Tagelus californianus*, the jackknife clam, could be confused with *Siliqua patula*. It too has nearly central beaks, is about 2.5 times as long as wide, and gapes at both ends. It never has the internal strengthening rib of *S. patula*, however, and its ligament is seated on a nymph or projection (as in *Protothaca staminea*, see plate). *Tagelus californianus* is gray, has no lateral teeth, and has short siphons (Coan and Carlton 1975). It is found below Humboldt Bay, California, in mudflats.

Ecological Information

Range: *Siliqua patula* was described from individuals collected near Coal Harbor, Cook Inlet, Alaska (Weymouth et al. 1926). Known range includes Aleutian Islands to Pismo Beach, California, but individuals are

uncommon in California (Weymouth et al. 1931).

Local Distribution: Coos Bay distribution at Pt. Adams spit near the mouth of the bay and usually on open coast. This species is more common in coastal regions with long stretches of wide sandy beaches (e.g., Seaside, OR, Connolly 1995).

Habitat: Flat, open beaches with fine, clean sand in strong surf zone with aeration (Anonymous 1968; Haderlie and Abbott 1980). This niche is occupied further south by the Pismo clam, *Trivela stultorum* (Ricketts and Calvin 1971).

Salinity: Collected at salinities of 30 or more, in full strength seawater.

Temperature: Lives in cold to temperate waters.

Tidal Level: Low intertidal to shallow subtidal (Haderlie and Abbott 1980), about - 0.3 meters and lower (Kozloff 1993).

Associates: Known associates include the olive snail, *Olivella biplicata*, caprellid amphipods, and polychaetes (e.g., *Ophelia*). The commensal nemertean, *Malacobdella grossa*, occurs in up to 80% of the clams (Fig. 1a) (Ricketts and Calvin 1952; Haderlie and Abbott 1980). These nemerteans are found attached to the clam's gills with their posterior sucker and they feed on planktonic organisms in the water that is passed over the gill surface; there is believed to be no harmful effect (Ricketts and Calvin 1952; Kozloff 1991).

Abundance: Populations can be very abundant in certain locals, but they move and fluctuate, which may be due to sand movement from storms and surf. Densest groups occur near mean low water (Anonymous 1968). Up to 10,123 clams/m² were reported in British Columbia, Canada (see Table 6, Bourne and Quayle).

Life-History Information

Reproduction: Separate sexes with broadcast spawning and external fertilization. Females produce 6–10 million eggs. In Washington, all individuals spawn suddenly and simultaneously near the end of May or early June, when water temperatures rise (e.g., 13°C, Fraser 1936; Ricketts and Calvin 1952; Haderlie and Abbott 1980). However, spawning is not sudden or simultaneous in Alaska or British Columbia, Canada, where spawning occurs from July to August (Ricketts

and Calvin 1952; Bourne and Quayle 1970; Breese and Robinson 1981, Lassuy and Simons 1989. Sperm morphology appears to characterize many veneroid taxa (see Fig. 2, Healy 1995).

Larva: Bivalve development, including members of the Pholadidae, generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the “D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone. Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig. 1, Kabat and O’Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001.) Swimming larval duration is up to eight weeks (Ricketts and Calvin 1952; Haderlie and Abbott 1980). Larvae of *Siliqua patula* are free swimming, but they often stay close to sediment surface (Haderlie and Abbott 1980). After metamorphosis, individuals are the size of wheat grain or smaller and reach to 1.5 cm by end of the “growing season” in December (Washington, Anonymous 1968).

Juvenile: Juveniles have an oval shell outline until they are about 2.5 mm in length (Pohlo 1963). Individuals are with central beak, but not elongate (see Fig. 6, Pohlo 1963). Eighty-six percent of third year clams (approximately 10 cm in length) are sexually mature or maturing (Queen Charlotte Island, Fraser 1936). In British Columbia, clams reached 90 mm by about 1.5–3 years old (Bourne and Quayle 1970).

Longevity: 12 (Washington) to 19 years of age (Alaska) (Ricketts and Calvin 1952; Haderlie and Abbott 1980); little growth is seen after 15 years (Alaska, Haderlie and Abbott 1980). The largest individuals in California were nine years old (Haderlie and

Abbott 1980). Mortality is high among young individuals (reaching up to 99%), with greatest losses after major storms (Anonymous 1968).

Growth Rate: Growth can be measured by annual shell rings; growing seasons show as wide brown areas between rings. Growth proceeds as follows: 20 mm in first year, 130 mm after 5 years, and 160 mm after 13 years (Haderlie and Abbott 1980). Individuals reach 11.5 cm in length by approximately 3.5 years (Washington). Washington and California (e.g., Pismo) individuals grow rapidly, but do not reach as large a size or live as long as they do in Alaska (Chignik Bay, Weymouth et al. 1926; Ricketts and Calvin 1952). Growth rates tend to slow after 10 cm sizes are reached (Weymouth and McMillin 1931). Winter shell lengths were measured in Long Beach, British Columbia, Canada and were 37mm, 91mm, 112.5 mm, 123 mm, and 131mm in years 1–5, respectively (Bourne and Quayle 1970).

Food: A filter feeder of planktonic diatoms. *Siliqua patula* concentrates phytoplankton and, at the same time, concentrates some species that are associated with harmful algal blooms (e.g., *Pseudo-nitzschia*). Toxins (domioc acid) within their tissues can be dangerous if ingested by humans (Horner et al. 1997; Dortch et al. 1997; Kumar et al. 2009; Chadsey et al. 2012).

Predators: *Siliqua patula* is probably the most highly prized food mollusk in the northwest, thus this species has been extensively harvested both recreationally and commercially. Unrestricted in 1925, harvesting severely harmed populations (Weymouth and McMillin 1931) and lead to a downward trend. In 1976, Oregon total harvest was 2,211,000 clams (Link 1977). Additional predators include seagulls, ducks, perch, crab, and fish (e.g. Starry flounder) (Anonymous 1968; Haderlie and Abbott 1980). Interestingly, DNA sequence data revealed that razor clam species in the commercially harvested genus *Ensis* are often mislabeled as congeneric cryptic species with sympatric distributions (Esperina et al. 2009; Vierna et al. 2013).

Behavior: *Siliqua patula* is known for its quick, efficient digging (see **Burrow**). Individuals move especially rapidly in the second or "slosh" layer of sand (Anonymous 1968). Digging is accomplished by the ability

of the anchor-shaped foot to change shape. Extraordinary muscle capacity and the displacement of body fluids are responsible for this (Pohlo 1963; Kozloff 1993). Digging is vertical, and is sometimes angled toward the sea with very little horizontal movement. Individuals 3 to 8 cms in length bury themselves within 7 and 27 seconds, respectively (Pohlo 1963).

Bibliography

1. ADAMS, N. G., M. LESOING, and V. L. TRAINER. 2000. Environmental conditions associated with domoic acid in razor clams on the Washington coast. *Journal of Shellfish Research*. 19:1007-1015.
2. ANONYMOUS. 1968. Invertebrate fisheries, p. 35-49. Department of Fish and Wildlife, Oregon State University, Corvallis, OR.
3. BISHOP, J. A. 2000. A record size for the razor clam *Siliqua patula*. *Festivus*. 32:77-78.
4. BOURNE, N. 1979. Razor clam, *Siliqua patula* Dixon, breeding and recruitment at Masset, British Columbia. *Proceedings of the National Shellfisheries Association*. 69:21-29.
5. BOURNE, N., and D. B. QUAYLE. 1970. Breeding and growth of razor clams in British Columbia. Technical Report of the Fisheries Research Board of Canada. No. 232:1-42.
6. BREESE, W. P., and A. ROBINSON. 1981. Razor clams, *Silqua patula* (Dixon): gonadal development, induced spawning and larval rearing. *Aquaculture*. 22:27-33.
7. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
8. CHADSEY, M., V. L. TRAINER, and T. M. LESCHINE. 2012. Cooperation of science and management for harmful algal blooms: domoic acid and the Washington coast razor clam fishery. *Coastal Management*. 40:33-54.
9. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal*

- invertebrates from central California to Oregon. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
10. CONNOLLY, T. J. 1995. Archaeological evidence for a former bay at Seaside, Oregon. *Quaternary Research*. 43:362-369.
 11. DIXON, G. 1789. A voyage around the world. George Goulding, London.
 12. DORTCH, Q., R. ROBICHAUX, S. POOL, D. MILSTED, G. MIRE, N. N. RABALAIS, T. M. SONIAT, G. A. FRYXELL, R. E. TURNER, and M. L. PARSONS. 1997. Abundance and vertical flux of *Pseudo-nitzschia* in the northern Gulf of Mexico. *Marine Ecology Progress Series*. 146:249-264.
 13. DRUM, A. S., T. L. SIEBENS, E. A. CRECELIUS, and R. A. ELSTON. 1993. Domoic acid in the Pacific razor clam, *Silqua patula* (Dixon, 1789). *Journal of Shellfish Research*. 12:443-450.
 14. ELSTON, R. A., and M. G. PEACOCK. 1984. A Rickettsiales-like infection in the Pacific razor clam, *Silqua patula*. *Journal of Invertebrate Pathology*. 44:84-96.
 15. ESPINEIRA, M., J. M. VIEITES, and F. J. SANTA CLARA. 2009. Development of a method for the genetic identification of commercial bivalve species based on mitochondrial 18S rRNA sequences. *Journal of Agricultural and Food Chemistry*. 57:495-502.
 16. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 17. HEALY, J. M. 1995. Comparative spermatozoal ultrastructure and its taxonomic and phylogenetic significance in the bivalve order Veneroida. *Memoires du Museum National d'Histoire Naturelle*. 166:155-166.
 18. HERTLEIN, L. G. 1961. A new species of *Silqua* (Pelecypoda) from western North America. *Bulletin of the Southern California Academy of Sciences*. 60:12-19.
 19. HIRSCHHORN, G. 1962. Growth and mortality rates of the razor clam (*Silqua patula*) on Clatsop Beaches, Oregon. *Contributions Oregon Fish Commission*. No. 27:1-55.
 20. HORNER, R. A., D. L. GARRISON, and F. G. PLUMLEY. 1997. Harmful algal blooms and red tide problems on the US west coast. *Limnology and Oceanography*. 42:1076-1088.
 21. HORNER, R. A., and J. R. POSTEL. 1993. Toxic diatoms in western Washington waters (US west coast). *Hydrobiologia*. 269:197-205.
 22. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 23. KEEN, A. M. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. Stanford University Press, Stanford, CA.
 24. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
 25. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 26. KUMAR, K. P., S. P. KUMAR, and G. A. NAIR. 2009. Risk assessment of the amnesic shellfish poison, domoic acid, on animals and humans. *Journal of Environmental Biology*. 30:319-325.
 27. LASSUY, D. R., and D. SIMONS. 1989. Species profiles, life histories and environmental requirements of coastal fish and invertebrates: Pacific Northwest. Pacific razor clam. US Fish and Wildlife Service Biological Report. 82:I-VI, 1-16.
 28. LECLAIR, L. L., and S. R. PHELPS. 1994. Genetic characteristics and relationships of five razor clam (*Silqua patula*, Dixon) populations along the Pacific coast of North America.

- Journal of Shellfish Research. 13:207-216.
29. MCLACHLAN, A., J. E. DUGAN, O. DEFEO, A. D. ANSELL, D. M. HUBBARD, E. JARAMILLO, and P. E. PENCHASZADEH. 1996. Beach clam fisheries. *Oceanography and Marine Biology*. 34:163-232.
 30. OLDROYD, I. S. 1924. Marine shells of Puget Sound and vicinity. University of Washington Press, Seattle.
 31. POHLO, R. H. 1963. Morphology and mode of burrowing in *Siliqua patula* and *Solen rosaceus* (Mollusca: Bivalvia). *Veliger*. 6:98-104.
 32. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides: an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford: Stanford University Press, Stanford.
 33. TAYLOR, C. C. 1959. Temperature and growth: the Pacific razor clam. *Journal du Conseil*. 25:93-101.
 34. VIerna, J., J. CUPERUS, A. MARTINEZ-LAGE, J. M. JANSEN, A. PERINA, H. VAN PELT, and A. M. GONZALEZ-TIZON. 2014. Species delimitation and DNA barcoding of Atlantic *Ensis* (Bivalvia, Pharidae). *Zoologica Scripta*. 43:161-171.
 35. VON COSEL, R. 1992. *Solen rosaceus*: three species. *Veliger*. 35:366-380.
 36. WEKELL, J. C., E. J. GAUGLITZ, JR., H. J. BARNETT, C. L. HATFIELD, D. SIMONS, and D. AYRES. 1994. Occurrence of domoic acid in Washington State razor clams (*Siliqua patula*) during 1991-1993. *Natural Toxins*. 2:197-205.
 37. WEYMOUTH, F. W., and H. C. MCMILLIN. 1931. The relative growth and mortality of the Pacific razor clam (*Siliqua patula* Dixon), and their bearing on the commercial Fishery. *Bulletin, Fishery Bulletin*. 46:543-567.
 38. WEYMOUTH, F. W., H. C. MCMILLIN, and H. B. HOLMES. 1926. Growth and age at maturity of the Pacific razor clam, *Siliqua patula* (Dixon). *Fishery Bulletin*. 41:201-236.
 39. WEYMOUTH, F. W., H. C. MCMILLIN, and W. A. RICH. 1931. Latitude and relative growth in the razor clam *Siliqua patula*. *Journal of Experimental Biology*. 8:228-249.

Updated 2016

Solen sicarius

The sickle razor clam, or blunt jackknife clam

Phylum: Mollusca
Class: Bivalvia, Heterodonta
Order: Veneroida
Family: Solenidae

Description

Size: Individuals up to 125 mm in length (Haderlie and Abbott 1980; Kozloff 1993). The illustrated specimen (from Coos Bay) is 90 mm in length, which is the same size as reported type specimens (Oldroyd 1924; Ricketts and Calvin 1952).

Color: Shell very white in color, but covered with yellow green, and glossy periostracum (Ricketts and Calvin 1952). The foot can be darkly pigmented (Kozloff 1993).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Solenid and pharid bivalves are burrowers and some species are quite fast (e.g. *Siliqua patula*, see description in this guide). They have shells that are longer than wide and often razor-like at the opening edge (see Plate 397G, Coan and Valentich-Scott 2007).

Body: Long, dark and finger-like body. The posterior end swells to form an anchor (see Fig. 306 Kozloff 1993).

Color:

Interior: The mantle is fused along the entire ventral margin and restricts foot movement along anterior-posterior axis (Pohlo 1963), but serves as a barrier to outside foreign material. The ligament is long, entirely external, and not seated on nymph (Figs. 2, 4).

Exterior:

Byssus:

Gills:

Shell: Shell is slightly bent, elongate, and gapes at both ends. The dorsal margin is slightly concave and has beaks near the anterior end. The anterior margin is blunt while the posterior is rounded (Ricketts and Calvin 1952; Haderlie and Abbott 1980).

Interior: Adductor scars at opposite ends of shell and the anterior scar is elongate, while the posterior is oblong (Oldroyd 1924). The pallial sinus is shallow

(Coan and Valentich-Scott 2007) and the pallial line extends beyond the anterior adductor scar. In the illustrated specimen, the line is a strong rib (Fig. 2), however there is no strong radial rib as in some Solenidae.

Exterior: Shell shape is cylindrical (solen = channel pipe, Quayle 1970). Length about four times the width and gapes at both ends (Coan and Valentich-Scott 2007). The shell is thin, the valves are moderately inflated, beaks are at near anterior end, and very weak (Figs. 1, 4). The dorsal margin is straight or slightly concave, but not arched (*Solen*, Keen and Coan 1974) (Fig. 1). The ventral margin is arched (Oldroyd 1924) and the anterior edge is truncate while the posterior is rounded.

Hinge: The hinge is close to anterior end (Kozloff 1993). Beaks are terminal and situated at anterior end (*Solen*, Keen 1971) (Figs. 1, 2, 4). One cardinal tooth is present in each valve and teeth are erect, recurved, and triangular (Oldroyd 1924).

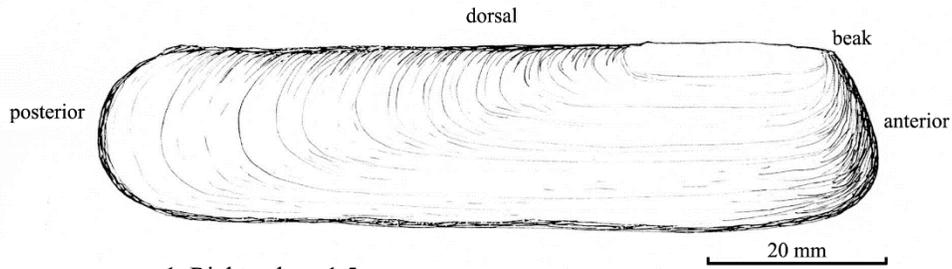
Eyes:

Foot: The foot is with dark pigment (Kozloff 1993) (Fig. 4).

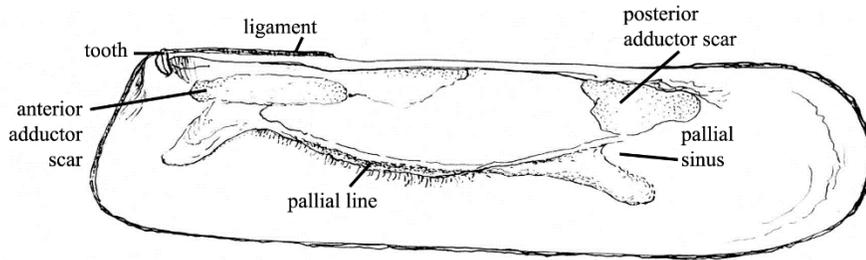
Siphons: Inhalant and exhalant siphons are joined (Fig. 4a). Siphons of both *Solen rostriformis* and *S. sicarius* can be readily autotomized at annular constrictions on the siphon (Ricketts and Calvin 1952; Pohlo 1963; Haderlie and Abbott 1980; Rudy and Rudy, personal observation). The siphon of the former species are even too large to be retracted completely into the shell (Ricketts and Calvin 1952).

Burrow: The burrow of *S. sicarius* is permanent, vertical, and reaches depths of 30–35 cm (Haderlie and Abbott 1980). Individuals dig rapidly and are very active, burying themselves completely within 30 seconds with four to five thrusts of the muscular **foot** (Ricketts and Calvin 1952; Haderlie and Abbott 1980).

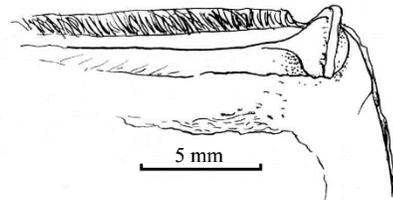
Solen sicarius



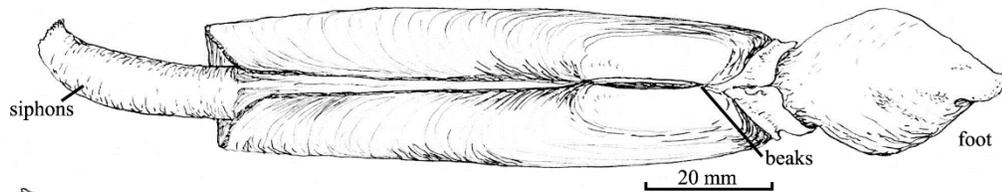
1. Right valve x1.5:
shell cylindrical; dorsal margin straight, anterior edge truncate;
length 4x width; beaks terminal, very weak; shell white,
periostracum yellow green, glossy.



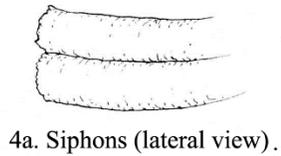
2. Right valve, internal:
adductor scars at opposite ends of shell; pallial
line a strong edge; no radial rib.



3. Hinge area, left valve x4:
a large single tooth (each valve).



4. Dorsal view x1.5.



4a. Siphons (lateral view).

Possible Misidentifications

Solenidae and Pharidae are two razor clam families represented locally and pharid genera were recently placed in the former family (see previous editions of this guide). They are both characterized by cylindrical shells that are about 2.5 times as long as high and gape at both ends. They have no dorsal margin ears (compare to Pectinidae, see Plate 394E, Coan and Valentich-Scott 2007), a hinge with ligament that is entirely external and dorsal, equally shaped adductor muscle scars (compare to *Mytilus trossulus*, this guide), and shells that do not have prominent radial sculpturing (Coan and Valentich-Scott 2007). The difference between the two families is that members of the Pharidae have one shell valve with two cardinal teeth and the other with four, while the Solenidae have a single cardinal tooth on each shell valve (Coan and Valentich-Scott 2007). Other local razor-shaped clams besides the Solenidae such as the Mytiidae include some genera (e.g., *Adula*) which are also long and cylindrical. *Adula* (see *A. californiensis*, this guide) are usually a boring species, however, having hairy posterodorsal slopes, a very small anterior adductor scar, and no hinge teeth (Coan and Valentich-Scott 2007). Hiatellidae, including the geoduck, *Panopea generosa* have large, quadrate, gaping bivalves, without hinge teeth, and with nearly equal adductor muscle scars (Keen and Coan 1974).

Only two species, in the genus *Solen*, are reported locally in the Solenidae, they have an almost straight dorsal margin, a terminal beak, and one cardinal tooth in each valve (Keen 1971). *Solen rostiformis* (= *S. rosaceus*, but see Pohlo 1963; von Cosel 1992) has a thin shell that tapers and a periostracum that is lighter than *S. sicarius*; it is light olive green to brown in color. *Solen rostiformis* is a pink shelled clam and its siphons are annulated (and it can regenerate them when disturbed, Pohlo 1963). It lives in sandier situations than does *S. sicarius* (Coan and Carlton 1975). *Solen sicarius*, on the other hand, has a thick shell, a blunt posterior ('the blunt razor shell') and a dark brown periostracum. *Solen sicarius* is found occasionally in permanent burrows in mud or muddy sand (Kozloff 1974) and is the species most likely to be confused with

Siliqua patula. It lacks an interior vertical rib and multiple hinge teeth, and is four times as long as wide, not 2.5 times, as in *S. patula* (Keen and Coan 1974). Furthermore, the profile in *S. patula* is much more oval, and not as cylindrical as in *Solen sicarius*.

Four species are reported locally in the Pharidae. *Siliqua patula* has an internal rib that slopes anteriorly, a wide and tapering posterior end. *Siliqua lucida* is smaller than *S. patula* (< 55 mm in length) and has an internal rib that is vertical and narrow and a posterior end that is truncate. It has been suggested that *S. lucida* are simply young *S. patula* individuals (Hertlein 1961), but this is not yet known. *Siliqua lucida* lives in protected bay sands and has concentric brown bands on its exterior. Although variations in *S. patula* have been synonymized, occasionally readers will find references to *S. patula* var. *nuttallii*, which is more oval shape, with purple beaks and four hinge teeth in the left valve, not two (Oldroyd 1924). *Ensis myrae* and *Siliqua altra* are offshore species and *E. myrae* has a shell that is long and thin.

Ecological Information

Range: Type locality is the Straits of Juan de Fuca. Known range extends from Vancouver Island, BC, Canada to San Quintin Bay, Baja California.

Local Distribution: Locally occurs in mudflats of both Coos Bay and Charleston.

Habitat: Individuals found in permanent vertical burrows of protected parts of bays, within mud or muddy sand (Coan and Valentich-Scott 2007). *Solen sicarius* is more common among eelgrass (e.g., *Zostera marina*) roots, in firm sediments than other mudflats.

Salinity: Collected at salinities of 30 in Coos Bay.

Temperature: Cold to warmer temperate waters.

Tidal Level: Low intertidal to shallow subtidal (Haderlie and Abbott 1980). In Coos Bay, individuals are primarily collected intertidally.

Associates: Known associates include the commensal pea crabs (e.g. *Pinnixa*, Quayle 1970).

Abundance: Not common, but becoming more abundant in Coos Bay (Rudy and Rudy, personal observation). In Inchon, Korea, a

population of the congeneric species, *S. strictus*, reached mean densities of 126 individuals/m² (Hong and Park 1994).

Life-History Information

Reproduction: Although little is known about the reproduction and development in *Solen sicarius*, reproductive aspects of biology have been studied for several congeners. *Solen marginatus*, a species that occurs on Spanish coasts, is reproductive from May to July (Spain, Remacha-Trivino and Anadon 2006) and in *Solen grandis*, spawning occurred from April to May. Several spawning events were observed for *S. dactylus*, in the northern Persian Gulf, from August to February (Saeedi et al. 2009). The sperm morphology of the congeners *S. cylindraceus* and *S. capensis* was studied by Hodgson et al. (1987). In both species, sperm were of “primitive type” (i.e., typical triangular shape that is not elongated in any way), with head pieces approximately 1.5µm in length, but acrosome morphology was species specific. In fact, sperm morphology appears to characterize many veneroid taxa (see Fig. 2, Healy 1995). Fertilized oocytes of *S. marginatus* were approximately 156 µm in diameter and surrounded by a chorion (da Costa and Martinez-Patino 2009) and mature oocytes of *S. gordonis* and *S. strictus* from Dadaepo, Pusan, Korea were 80–90 µm (Chung et al. 1986).

Larva: Bivalve development, including members of the Pholadidae, generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the “D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone. Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of

the velum, it is called a pediveliger (see Fig. 1, Kabat and O’Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001.) In *Solen grandis*, D-shaped larvae hatched after 20 hours and were 125 µm. After 5–6 days, larvae were early umbo stage and approximately 250 µm (Guo-qiang et al. 2009). Settlement occurred after nine days in *Solen marginatus* when larvae were approximately 300 µm (da Costa and Martinex-Patino 2009).

Juvenile:

Longevity:

Growth Rate: In the congener, *Solen marginatus*, seed were 19 mm at four months and one year old juveniles were 38.5 mm. After three years, individuals were 80 mm (da Costa and Martinez-Patino 2009).

Food: A suspension and filter feeder.

Predators: Known predators include birds (e.g., white-winged scoter, Grosz and Yocom 1972) and sea stars (e.g., *Pisaster brevispinus*, Sloan and Robinson 1983).

Behavior: A very good digger, it can bury itself in 30 seconds. However, *S. sicarius* is not as fast a burrower as *S. patula*: an individual 7 cm in length requires 45 seconds to 11 min to bury itself (compare to 7–27 seconds for *S. patula*, see description in this guide) (Pohlo 1963). Interestingly, *Solen sicarius* can also both swim and jump (MacGinitie 1935). They do so by either expelling water from their siphons rapidly or through the opening surrounding the siphon. With these techniques they are able to move up to two feet through the water or use the blast of water to soften sediments for rapid burrowing (Ricketts and Calvin 1952; Haderlie and Abbott 1980).

Bibliography

1. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In*: Identification guide to larval marine invertebrates of the Pacific Northwest. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
2. CHUNG, E. Y., H. B. KIM, and T. Y. LEE. 1986. Annual reproductive cycle of the jackknife clams, *Solen strictus* and *Solen gordonis*. Bulletin of the Korean Fisheries Society. 19:563-574.

3. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon.* J. T. Carlton (ed.). University of California Press, Berkeley, CA.
4. DA COSTA, F., and D. MARTINEZ-PATINO. 2009. Culture potential of the razor clam *Solen marginatus* (Pennant, 1777). *Aquaculture.* 288:57-64.
5. GROSZ, T., and C. F. YOCOM. 1972. Food habits of white winged scoter in northwestern California. *Journal of Wildlife Management.* 36:1279-1282.
6. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California.* R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
7. HEALY, J. M. 1995. Comparative spermatozoal ultrastructure and its taxonomic and phylogenetic significance in the bivalve order Veneroida. *Memoires du Museum National d'Histoire Naturelle.* 166:155-166.
8. HODGSON, A. N., C. J. DEVILLIERS, and R. T. F. BERNARD. 1987. Comparative spermatology of two morphologically similar species of *Solen* (Mollusca, Bivalvia). *South African Journal of Zoology.* 22:264-268.
9. HONG, J., and H. PARK. 1994. Growth and production of macrobenthic fauna on a macrotidal flat, Inchon, Korea I. Growth of the razor clam, *Solen strictus* (Bivalvia, Solenidae) from Chokchon tidal flat. *Bulletin of the Korean Fisheries Society.* 27:549-559.
10. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast.* M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
11. KEEN, A. M. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. Stanford University Press, Stanford, CA.
12. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
13. MACGINITIE, G. E. 1935. Ecological aspects of a California marine estuary. *American Midland Naturalist.* 16:629-765.
14. OLDROYD, I. S. 1924. Marine shells of Puget Sound and vicinity. University of Washington Press, Seattle.
15. POHLO, R. H. 1963. Morphology and mode of burrowing in *Siliqua patula* and *Solen rosaceus* (Mollusca: Bivalvia). *Veliger.* 6:98-104.
16. QUAYLE, D. B. 1970. The intertidal bivalves of British Columbia. British Columbia Provincial Museum, Victoria, BC, Canada.
17. REMACHA-TRIVINO, A., and N. ANADON. 2006. Reproductive cycle of the razor clam *Solen marginatus* (Pulteney 1799) in Spain: A comparative study in three different locations. *Journal of Shellfish Research.* 25:869-876.
18. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
19. SAEEDI, H., S. P. RAAD, A. A. ARDALAN, E. KAMRANI, and B. H. KIABI. 2009. Growth and reproduction of *Solen dactylus* (Bivalvia: Solenidae) on northern coast of the Persian Gulf (Iran). *Journal of the Marine Biological Association of the United Kingdom.* 89:1635-1642.
20. SLOAN, N. A., and S. M. C. ROBINSON. 1983. Winter feeding by asteroids on a subtidal sandbed in British Columbia. *Ophelia.* 22:125-141.
21. VON COSEL, R. 1992. *Solen rosaceus*: three species. *Veliger.* 35:366-3

Updated 2016

Macoma balthica

Phylum: Mollusca
Class: Bivalvia; Heterodonta
Order: Veneroida
Family: Tellinidae

Taxonomy: Originally described as a member of the genus *Tellina*, *Macoma balthica* was the name of the Atlantic species. Our west coast clam was originally called *M. inconspicua* (Broderip and Sowerby 1829), but they are now generally considered to be the same species (e.g., Vassallo, 1969, 1971; Haderlie and Abbott 1980). An extensive taxonomic history has yielded many synonyms for *M. balthica*. Some ambiguity exists whether individuals from the southernmost reaches of the distribution on east and west sides of the Atlantic should be considered the same species (Beukema and Meehan 1985) and some researchers (e.g., Meehan 1985; Kamermans et al. 1990; Luttkhuizen et al. 2012; Sanier et al. 2015) consider these allopatric populations to be subspecies (eastern Atlantic *Macoma balthica balthica* and western Atlantic *Macoma balthica rubra*) that have been reproductively isolated for 2–3.5 million years (Luttkhuizen et al. 2012; Saunier et al. 2015). *Macoma petalum* populations in San Francisco Bay, once recognized as distinct species from *M. balthica* (Vainola 2003), are now believed to be genetically identical to *Macoma balthica* (the circum-Arctic species) (Brusati and Grosholz 2007). However, these may yet prove different species and their taxonomy awaits further study (Coan and Valentich-Scott 2007; Brusati and Grosholz 2007). Thus, the description below considers them together as is done in current local intertidal guides (e.g. Coan and Valentich-Scott 2007). (see Vainola 2003 for molecular systematics of *M. balthica* species complex.)

Description

Size: Individuals averaging 30–35 mm in length (Oldroyd 1924), but usually under 30 mm (Coan 1971) and rarely more than 45 mm (Coan 1971; Cardoso et al. 2003). Smallest adults are 2 mm (Caddy 1969). Body proportions are generally 27 in length, 22 in height, and 11 mm in diameter (Oldroyd 1924). The illustrated specimen (from Coos Bay) is 17.5 mm long.

Color: Distinct color is reddish, pale rose or white and is sometimes bluish or yellow (Oldroyd 1924; see Plate 17, Kozloff 1993). Coos Bay specimens are usually pink inside and out, but individuals from British Columbia, Canada can have pink or yellow interiors (Quayle 1970).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Among the bivalves, the Heterodonta are characterized by **ctenidia** (or gills) that are eulamellibranchiate, fused mantle margins and the presence of long **siphons**. Veneroid bivalves have well-developed hinge teeth and members of the family Tellinidae have short lateral hinge teeth (when present – see **Possible Misidentifications**), shells with external striations or ribs, and deep pallial sinuses (Coan and Valentich-Scott 2007). When holding closed shell in both hands with the hinged area up and the ligaments toward you, the right valve is in the right hand (Fig. 3) (Keen and Coan 1974).

Body:

Color:

Interior: Ligament is short, but strong, partially sunken, seated on a stout callus (Dunnill and Ellis 1969), but not on a nymph (Tellinidae, Coan and Valentich-Scott 2007).

Exterior:

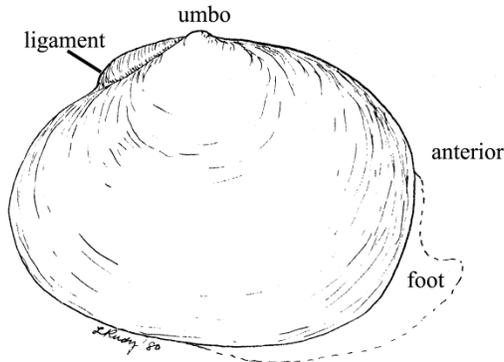
Byssus:

Ctenidia:

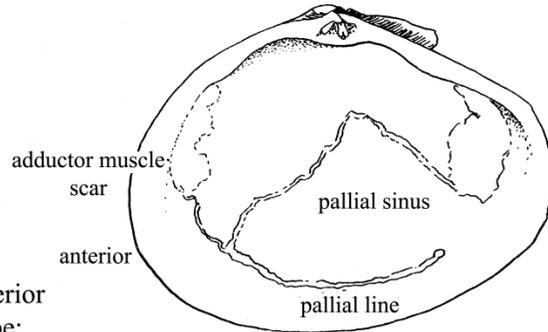
Shell: The shell shape is regularly oval, round, thick, with equal valves, umbos low, almost central, and usually worn (Fig. 1). The dorsal margin is arched, the ventral margin is slightly contracted (Oldroyd 1924), and there is no posterior dorsal flange (posterior to ligament). Valves do not gape (Tellinidae, Keen 1971) and the posterior end is rounded. Shell usually heavy, but bay specimens sometimes thin (Coan 1971).

Interior: Pallial line is narrow and faint. The pallial sinus is large (see Plate 422,

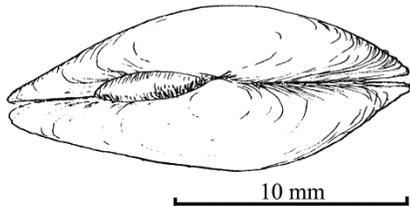
Macoma balthica



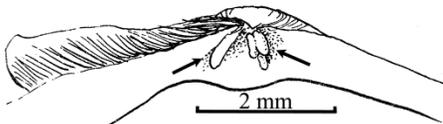
1. *Macoma balthica*, exterior, right valve (L:17.5mm,D:7.5mm,H:14mm) x4: shell regular, oval; valves equal; umbos low, almost central; anterior and posterior ends rounded: no flange, bend or gape; exterior color pink; ligament external, short, strong.



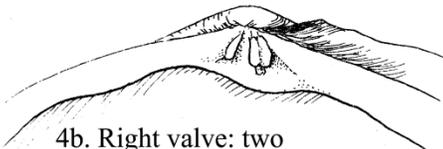
2a. Interior, right valve: pallial line narrow, faint; pallial sinus ends 3/4 of way to anterior adductor muscle scar; sinuses in both valves similar; interior pink.



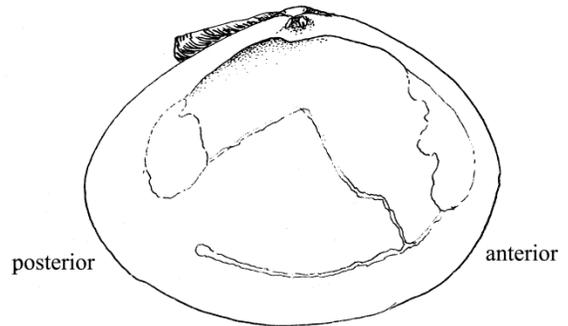
3. (Dorsal view) x4: valves not bent.



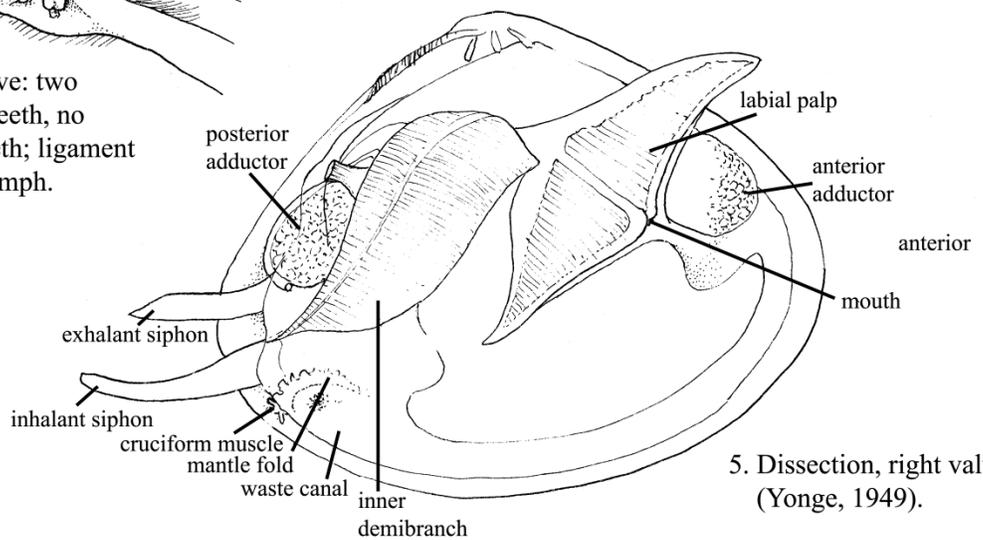
4a. Left valve x12: two cardinal teeth, no lateral teeth.



4b. Right valve: two cardinal teeth, no lateral teeth; ligament not on nymph.



2b. Left valve



5. Dissection, right valve: (Yonge, 1949).

Coan and Valentich-Scott 2007) and equal among valves. The sinus ends $\frac{3}{4}$ of the way to anterior adductor muscle scar in both valves (Figs. 2a, 2b), and does not reach the muscle scar (Fig. 2b) (Coan and Valentich-Scott 2007).

Exterior: Periostracum is thin, silky, not shiny (Coan 1971), and a trace is visible only ventrally. Shell sculpture consists of fine concentric growth lines only (Figs. 1, 3) (Dunnill and Ellis 1969).

Hinge: The hinge area has no lateral teeth (*Macoma*, Coan and Valentich-Scott 2007). Two cardinal teeth exist in each valve (Figs. 4a, 4b), one stout, bifid, and the other single and fragile (Dunnill and Ellis 1969).

Eyes:

Foot:

Siphons: The siphons are long, separate, and mobile (Kozloff 1993). Inhalant siphons are four times the shell length, when extended. Exhalant siphons held vertically above surface are 1.5 cm. Siphons bear large palps, for sorting fine particles (Fig. 5) (Yonge 1949). (For diagrams of siphon development, see Figs. 3, 6, Caddy 1969.)

Burrow:

Possible Misidentifications

Tellinids can be distinguished from other small or young bay clams (i.e., Mactridae: *Tresus*; Veneridae: *Protothaca*, *Saxidomus*; Myidae: *Mya*, *Cryptomya*) an external ligament, an ovate shell, an inconspicuous nymph (or supporting projection for the external ligament), sometimes reddish hue and lateral teeth as well as a shell with ribs or striations (no radial pattern) and shells that never gape. Lateral teeth may or may not be present in the Tellinidae (Coan 1971). Myids have a hinge with a spoon-shaped chondrophore (left valve) and a projecting tooth (right valve) (see *Mya arenaria*, this guide). Venerids have three cardinal teeth in each valve. Mactrids have an internal ligament, A-shaped cardinal teeth, and gaping valves (Coan and Valentich-Scott 2007). The Tellinidae has around 16 species distributed between two genera locally – *Tellina* and *Macoma*. These genera can be differentiated by the hinge teeth, *Tellina* species have a hinge with lateral teeth, while *Macoma* species do not. *Macoma* species have shells that are also more rounded and inflated than *Tellina*, and are smooth, white, often

chalky. They are characterized by having a ovate shell consisting of two equal valves, a dark and deciduous periostracum, two cardinal teeth, the absence of lateral teeth and a pallial sinus that is deeper on the left valve (Scott and Blake 1998; Arruda and Domaneschi 2005). *Macoma* species may also have a more northern geographic distribution while *Tellina* are elongate, relatively compressed, conspicuously sculptured, brightly colored, and usually warm water dwellers (Coan 1971). Eleven species in the infaunal genus *Macoma* (Luttikhuisen et al. 2012) are reported locally (although 30 have been identified in the northeastern Pacific, Dunnill and Ellis 1969), but only seven are described in local keys (e.g. Coan and Valentich-Scott 2007), the four most common species of *Macoma* in our area are *M. balthica*, *M. nasuta*, *M. inquinata*, and *M. secta* (Kabat and O'Foighil 1987).

Two species, *M. secta* and *M. indentata* have a posterior dorsal flange extending from posterior end to the external ligament, this is absent in other *Macoma* species. The former species is called the sand clam and has a quadrate and truncate posterior. The latter is elongate, has a pointed posterior, unique muscle scars, is relatively rare and small (to 2.5 cm) and occurs from Trinidad, California southward. *Macoma secta*, also has a white shell, with a yellowish epidermis. Its right valve is more inflated than the left, and it can be large (to 120 mm) and is more common in clean sand, not in estuarine mud.

The morphology of the pallial sinus differentiates the other species. In species without a posterior dorsal flange, *M. acolasta* and *M. yoldiformis*, the anterior ventral edge of the pallial sinus is detached for a portion of the distance to the posterior adductor muscle scar. *Macoma acolasta* also has a rounded posterior, rather than pointed as in *M. yoldiformis* and is rare, sand-dwelling, and occurs from Bodega Bay, California, southward. *Macoma yoldiformis* is elongate, inflated, and thin, with the pallial sinus detached from the pallial line. Although the range of this clam is from Vancouver south to Baja California, it is not included in Puget Sound or British Columbia work (Dunnill and Ellis 1969). It can be found in silt in low intertidal of protected bays (Coan and Valentich-Scott 2007).

Macoma inquinata, *M. nasuta* and *M. balthica* (see descriptions in this guide) are all species with an anterior ventral edge of pallial sinus that is not detached and they tend to be larger (up to 110 mm) than *M. acolasta* or *M. yoldiformis* (less than 30 mm). *Macoma balthica* has a pinkish hue and a pallial sinus that ends $\frac{3}{4}$ of the way to anterior adductor muscle scar and is generally more oval than *M. nasuta* or *M. inquinata* (compare Fig. 1 *M. balthica*, with Fig. 1 *M. nasuta*, this guide) (Kozloff 1993). In *M. inquinata*, the pallial sinus does not reach the ventral end of the anterior adductor muscle and the shell is chalky white with a fibrous olive green periostracum. *Macoma nasuta*, on the other hand, is not as round and heavy as *M. inquinata* and its pallial sinus reaches and joins the anterior adductor scar above its base (left valve). (Its right valve may be more like *M. inquinata*'s). Furthermore, its siphons are orange and its shell posterior is bent to the right. *Macoma inquinata* can also bend slightly posteriorly, and may be confused with the thinner *M. nasuta*, without investigations of the other aforementioned features. (see Plate 422 for diagrams of these distinguishing characteristics in *Macoma*). *Macoma balthica* and *M. inquinata* are generally smaller than *M. nasuta* (up to 5 cm), with mature *Macoma balthica* rarely exceeding 25 mm in length (Dunnill and Ellis 1969), but could be confused with the young of some of these larger clams. Molecular differences have been documented within the *M. balthica* complex (see Vainola 2003) as well as morphological differences between the eastern (*Macoma balthica balthica*) and western (*Macoma balthica rubra*) Atlantic populations or subspecies. In particular, populations from southeastern United States estuaries exhibited larger shells and higher siphon height, which may correspond to deeper burying depths to avoid higher water temperatures in this region (Kamermans et al. 1990).

(The following species may be present locally, but are not included in local dichotomous keys). *Macoma expansa*, is a rare, usually offshore species (to 50 mm) whose pallial sinuses are perpendicular to the pallial line. *Macoma elimata* is found in 15–476 meters of water. *Macoma incongrua* is a generally northern species which can be found to 33°N latitude, intertidally to 36

meters. It has somewhat inflated valves, is usually 30–40 mm long, and almost round in outline (Dunnill and Ellis 1969). *Macoma calcarea* is found from 35 meters and lower, from 37° northward. Other northern subtidal species include the large *M. brota* and *M. lipara* (Dunnill and Ellis 1969).

Ecological Information

Range: Type locality is the Baltic Sea. *Macoma balthica* is present in the North Pacific and North Atlantic, in both European and North American waters. In Europe, distribution includes the White Sea, Pechora Sea, Wadden Sea, and southern coastal France. North American distribution includes the Gulf of St. Lawrence and Hudson Bay, south to Virginia as well as the Alaskan coast to San Francisco, but rarely further south to San Diego (Coan 1971). This species was possibly introduced to San Francisco from the Atlantic coast (Coan and Valentich-Scott 2007). However, some hybridization between populations has been observed where they meet at the Baltic Sea (Luttikhuisen et al. 2012). Local genetic population structure with depth has been determined in the Gulf of Gdańsk in Poland (Becquet et al. 2013). **Local Distribution:** Coos Bay sites at the South Slough channel and airport spoil islands. Oregonian distribution in Siletz, Nestucca, Siuslaw, Netarts, Tillamook Bays and generally all bays within close proximity to the open coast (Hancock 1979; Kozloff 1993).

Habitat: Offshore and bay mud (Kabat and O'Foighil 1987). Often in very fine and sometimes black, foul mud. Currents largely determine distribution, as they affect the settlement of sediment and degree of shelter. Although coarseness of sediment was found to not be a determining factor in distribution (see Vassalio 1969), individuals may prefer fine sediment, which increases the density of their food supply (e.g., micro-organism populations, Newell 1963). *Macoma balthica* recruitment was negatively effected by suction dredging, presumably due to the reduction and subsequent lack of accumulation of fine-grained sediment (Piersma et al. 2001).

Salinity: Collected at salinities of 30 and also found in brackish water (Vassalio 1969). Individuals found where salinity is as low as 5 (Jansson et al. 2013). Along the York River in

the Chesapeake Bay, higher abundance, predation and food availability was found upriver (salinity 5–10) than downriver (salinity 15–19), although recruitment was lowest upriver (Seitz 2011).

Temperature: *Macoma balthica* prefers cold to temperate waters and has a low tolerance to elevated temperatures (Wadden Sea, Beukema et al. 2009). Increases in seawater temperature and mild winters alter the onset of spawning and associated recruitment timing among *Macoma balthica* (Phillipart et al. 2003) and their predators in the Wadden Sea (Dekker and Beukema 2014). Increases in water temperature have also been shown to reduce body mass, which usually decreases in winter, but to a greater degree during mild versus cold winters (Honkoop and Beukema 1997).

Tidal Level: Intertidal and subtidal (Kabat and O’Foighil 1987). Individuals found at + 0.3 m (Coos Bay, Shore Acres) and down to 37 m (Coan 1971). An apparent correlation between clam size and depth distribution was reported, with the smallest animals closest to surface (Vassalio 1969), where distance from surface can be determined by siphon length (Vassalio 1971).

Associates: In San Francisco Bay, California associates include the whelk, *Busycotypus*, the gastropod *Nassarius*, capitellid and nereid polychaetes, the amphipod, *Ampelisca*, and bivalves, *Gemma* and *Mya* (Vassalio 1969). Individuals are sometimes host to gymnophallid trematode (metacercariae) parasites (e.g. *Gymnophallus somateriae*, *Lacunovermis conspicuus*, *Meiogymnophallus multigemmulus*, Swennen 1969; Ching 1973) as well as a protist parasite, *Perkinsus chesapeakei* (Coss et al. 2001; Burreson et al. 2005).

Abundance: Adults most abundant in the upper intertidal zone (1.3–2.6 m) (San Francisco Bay, California, Vassalio 1969), where they compose 55% of the total invertebrate community. Density may be determined by currents, fineness of deposits and micro-organism food (Haderlie and Abbott 1980). Individuals not very common in Puget Sound, Washington (Kozloff 1993), but quite common at many stations in Coos Bay, OR. Pelagic larval abundances as high as 12,000 larvae/m³ were reported in the Baltic Sea (Jansson et al. 2013). Larval abundance (determined by single step nested multiplex

PCR) in Isefjord, Denmark showed two peaks, one in the July and another at the end of August (Larsen et al. 2007). Juvenile densities of up to 5,000 individuals/m² were reported in June in the Thames estuary, England (Caddy 1969). Adult density correlates with egg size, where populations that are more dense produce smaller eggs (e.g., 224 individuals/m² produce eggs that are 100.5 µm whereas five individuals/m² produce eggs that are 108.5 µm in diameter, Luttikhuizen et al. 2011).

Life-History Information

Reproduction: Reproduction and development has been described for *M. balthica* (Europe, Caddy 1967, 1969; Lammens 1967). Egg size correlates with adult density (see **Abundance**) and ranges from 100.5–108.5 µm in diameter (Wadden and North Seas, Luttikhuizen et al. 2011). In the Netherlands, oocytes measured 97 µm and spawning occurred in short burst throughout March–April (at 10°C, Caddy 1967). Research on the effects of ocean acidification has found that reduction in pH (e.g. 7.5) negatively effects fertilization, and causes slower growth, and delayed metamorphosis, which occurs at smaller sizes and reduces pelagic survival (Van Colen et al. 2012; Jansson et al. 2013; Jansson et al. 2015).

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the “D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone (see Fig. 1, Caddy 1969). Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig. 1, Caddy 1969; Kabat and O’Foighil 1987; Brink 2001). (For

generalized life cycle see Fig. 1, Brink 2001). Some bivalve species (e.g. *Mytilus edulis*), including *M. balthica*, have two dispersal periods. The initial larval dispersal and settlement into the benthos, where larvae are 200–500 µm, is followed by potential dispersal from the benthos by thread drifting on long hyaline threads when young clams are 5–12 mm (Beukema and Vlas 1989). In *M. balthica*, advanced veliger larvae have a yellow shell that is 245–350 µm in length and is with red umbo and small prodissoconch II (Kabat and O'Foighil 1987; Brink 2001). Veliger shell shape in *M. balthica* is broadly rounded (see Fig. 4, Brink 2001). *Macoma nasuta* and *M. secta* are also known to have free swimming veliger larvae (Marriage 1954; Rae 1978, 1979; Brink 2001). Planktonic duration is probably 2–5 weeks and larvae settle at sizes between 300–330 µm. Significant research has been conducted on recruitment, growth, and general biology of *Macoma balthica* in the Dutch Wadden Sea. These studies found that larval recruitment is most successful in summers following severe winters due to reduced predation pressure from populations negatively influenced by cold temperature (e.g., *Crangon crangon*, *Carcinus maenas*, Beukema et al. 1998; Dekker and Beukema 2014; Dekker and Beukema 2014). Conversely, increases in winter temperatures reduce reproductive output and increase juvenile mortality suggesting that *Macoma balthica* populations will suffer with a warming climate (Wadden Sea, Philippart et al. 2003; Beukema et al. 2009). Highest recruitment was observed after cold winters and recruitment reportedly failed altogether after mild winters in the Wadden Sea (Honkoop et al. 1998) (see also **Temperature**).

Juvenile:

Longevity: Up to 30 years (Cardoso et al. 2003). Five years was reported from Rand Harbor, Massachusetts and up to 25 years in the Gulf of Finland (Gilbert 1973).

Growth Rate: Individual age is often estimated by the external rings on the shell as the rings are produced each winter when growth slows. However, these growth rings are likely overestimates of actual age and, thus, underestimates of growth rates (Cardoso et al. 2003). Seasonal growth was observed in European populations, where growth rate correlates to food supply (e.g.

chlorophyll and unicellular algae) and ranged from 5–7 mm and 10–25 mm/year in the western Wadden Sea (see Fig. 5, Beukema et al. 2002). Growth measured in the same region was 0.009–0.011 mm/day from March through April and reduced to 0.001–0.002 mm/day from July to September (Cardoso et al. 2003). Average maximum length was greater for North American populations than European (Gilbert 1973) and may be evidence for two sibling species (Kamermans et al. 1990). Growth rate depends on season and food availability in San Francisco Bay, California (Thompson and Nichols 1988) and is relatively constant throughout the year in Massachusetts, though slightly accelerated in the summer.

Food: A suspension feeder that also feeds on mud surface bacteria and detritus as well as on planktonic organisms at high tide (Braefield and Newell 1961; Newell 1963; Vassalio 1969; Oldroyd 1924). Thus, *M. balthica* switches between suspension and deposit feeding modes depending on local habitat (Tornroos et al. 2015). Individuals compete for food with the amphipod, *Ampelisca*. Each individual feeds in a 4 cm area (Braefield and Newell 1961) and an increase in individual weight between late winter and early summer is dependent on algal feeding in the Wadden Sea (Beukema et al. 2014).

Predators: Predators include shorebirds (e.g., eiders *Somateria mollissima*, oystercatchers *Haematopus ostralegus*, red knots *Calidris canutus*, Beukema et al. 2010) and starry flounder (Vassalio 1969; Cardoso et al. 2003). Predators of newly settled spat include, *Ampelisca* (Vassalio 1969) and top down predation on young *M. balthica* by the shrimp, *Crangon crangon* and the shore crab, *Carcinus maenas* have a negative effect on populations (Dekker and Beukema 2014).

Behavior: *Macoma balthica* is essentially static and a slower burrower than some other *Macoma* species (Yonge 1949), requiring 2½ minutes to bury itself (Braefield and Newell 1961). U-shaped tracks in mud suggest movement toward and away from the sun (Braefield and Newell 1961).

Bibliography

1. ARRUDA, E. P., and O. DOMANESCHI. 2005. New species of *Macoma* (Bivalvia: Tellinoidea: Tellinidae) from southeastern Brazil, and with description of its gross anatomy. *Zootaxa*:13-22.
2. BECQUET, V., R. LASOTA, E. PANTE, A. SOKOLOWSKI, M. WOLOWICZ, and P. GARCIA. 2013. Effects of fine-scale environmental heterogeneity on local genetic structure in *Macoma balthica* from the Gulf of Gdask (southern Baltic Sea). *Hydrobiologia*. 714:61-70.
3. BEUKEMA, J. J., G. C. CADEE, and R. DEKKER. 2002. Zoobenthic biomass limited by phytoplankton abundance: evidence from parallel changes in two long-term data series in the Wadden Sea. *Journal of Sea Research*. 48:111-125.
4. BEUKEMA, J. J., G. C. CADEE, R. DEKKER, and C. J. M. PHILIPPART. 2014. Annual and spatial variability in gains of body weight in *Macoma balthica* (L.): Relationships with food supply and water temperature. *Journal of Experimental Marine Biology and Ecology*. 457:105-112.
5. BEUKEMA, J. J., and R. DEKKER. 2014. Variability in predator abundance links winter temperatures and bivalve recruitment: correlative evidence from long-term data in a tidal flat. *Marine Ecology Progress Series*. 513:1-15.
6. BEUKEMA, J. J., R. DEKKER, and J. M. JANSEN. 2009. Some like it cold: populations of the tellinid bivalve *Macoma balthica* (L.) suffer in various ways from a warming climate. *Marine Ecology Progress Series*. 384:135-145.
7. BEUKEMA, J. J., R. DEKKER, and C. J. M. PHILIPPART. 2010. Long-term variability in bivalve recruitment, mortality, and growth and their contribution to fluctuations in food stocks of shellfish-eating birds. *Marine Ecology Progress Series*. 414:117-130.
8. BEUKEMA, J. J., and J. DEVLAS. 1989. Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. *Marine Ecology Progress Series*. 52:193-200.
9. BEUKEMA, J. J., P. J. C. HONKOOP, and R. DEKKER. 1998. Recruitment in *Macoma balthica* after mild and cold winters and its possible control by egg production and shrimp predation. *Hydrobiologia*. 375-76:23-34.
10. BEUKEMA, J. J., and B. W. MEEHAN. 1985. Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. *Marine Biology*. 90:27-33.
11. BRAEFIELD, A. E., and G. E. NEWELL. 1961. The behaviour of *Macoma balthica* (L.). *Journal of the Marine Biological Association of the United Kingdom*. 41:81-87.
12. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
13. BRODERIP, W. J., and G. B. SOWERBY. 1829. Observations on new or interesting mollusca contained, for the most part, in the Museum of the Zoological Society. *Zoological Journal*. 4:359-379.
14. BRUSATI, E. D., and E. D. GROSHOLZ. 2007. Effect of native and invasive cordgrass on *Macoma petalum* density, growth, and isotopic signatures. *Estuarine Coastal and Shelf Science*. 71:517-522.
15. BURRESON, E. M., K. S. REECE, and C. F. DUNGAN. 2005. Molecular, morphological, and experimental evidence support the synonymy of *Perkinsus chesapeaki* and *Perkinsus andrewsi*. *Journal of Eukaryotic Microbiology*. 52:258-270.
16. CADDY, J. F. 1967. Maturation of gametes and spawning in *Macoma balthica* (L.). *Canadian Journal of Zoology*. 45:955-965.
17. —. 1969. Development of mantle organs, feeding, and locomotion in postlarval *Macoma balthica* (L.) (Lamellibranchiata). *Canadian Journal of Zoology*. 47:609-617.

18. CARDOSO, J. F. M. F., S. SANTOS, J. I. J. WITTE, R. WITBAARD, H. W. VAN DER VEER, and J. P. MACHADO. 2013. Validation of the seasonality in growth lines in the shell of *Macoma balthica* using stable isotopes and trace elements. *Journal of Sea Research*. 82:93-102.
19. CHING, H. L. 1973. Description of *Gymnophallus somateriae* (Levinsen, 1881) from *Macoma inconspicua* and diving ducks from Vancouver, Canada. *Canadian Journal of Zoology*. 51:801-806.
20. COAN, E. V. 1971. The Northwest American Tellinidae. California Malacozoological Society, Berkeley.
21. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
22. COSS, C. A., J. A. F. ROBLEDO, G. M. RUIZ, and G. R. VASTA. 2001. Description of *Perkinsus andrewsi* n. sp isolated from the baltic clam (*Macoma balthica*) by characterization of the ribosomal RNA locus, and development of a species-specific PCR-based diagnostic assay. *Journal of Eukaryotic Microbiology*. 48:52-61.
23. DEKKER, R., and J. J. BEUKEMA. 2014. Phenology of abundance of bivalve spat and of their epibenthic predators: limited evidence for mismatches after cold winters. *Marine Ecology Progress Series*. 513:17-27.
24. DUNNILL, R. M., and D. V. ELLIS. 1969. Recent species of the genus *Macoma* (Pelecypoda) in British Columbia. National Museum of Canada, National Historical Papers. 45:1-34.
25. GILBERT, M. A. 1973. Growth rate, longevity and maximum size of *Macoma balthica* (L.). *Biological Bulletin*. 145:119-126.
26. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
27. HANCOCK, D. R., T. F. GAUMER, G. B. WILLEKE, G. P. ROBART, and J. FLYNN. 1979. Subtidal clam populations: distribution, abundance, and ecology. Oregon State University, Sea Grant College Program, Corvallis.
28. HONKOOOP, P. J. C., and J. J. BEUKEMA. 1997. Loss of body mass in winter in three intertidal bivalve species: An experimental and observational study of the interacting effects between water temperature, feeding time and feeding behaviour. *Journal of Experimental Marine Biology and Ecology*. 212:277-297.
29. HONKOOOP, P. J. C., J. VAN DER MEER, J. J. BEUKEMA, and D. KWAST. 1998. Does temperature-influenced egg production predict the recruitment in the bivalve *Macoma balthica*? *Marine Ecology Progress Series*. 164:229-235.
30. JANSSON, A., J. NORKKO, S. DUPONT, and A. NORKKO. 2015. Growth and survival in a changing environment: Combined effects of moderate hypoxia and low pH on juvenile bivalve *Macoma balthica*. *Journal of Sea Research*. 102:41-47.
31. JANSSON, A., J. NORKKO, and A. NORKKO. 2013. Effects of reduced pH on *Macoma balthica* larvae from a system with naturally fluctuating pH dynamics. *PLoS ONE*. 8:1-7.
32. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
33. KAMERMANS, P., H. W. VAN DER VEER, J. I. J. WITTE, and E. J. ADRIAANS. 1999. Morphological differences in *Macoma balthica* (Bivalvia, Tellinacea) from a Dutch and three southeastern United States estuaries. *Journal of Sea Research*. 41:213-224.
34. KEEN, A. M. 1971. Sea shells of tropical west America: marine mollusks from Baja California to Peru. Stanford University Press, Stanford, CA.

35. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
36. KOZLOFF, E. N. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
37. LAMMENS, J. J. 1967. Growth and reproduction in a tidal flat population of *Macoma balthica* (L.). Netherlands Journal of Sea Research. 3:315-382.
38. LARSEN, J. B., M. E. FRISCHER, K. W. OCKELMANN, L. J. RASMUSSEN, and B. W. HANSEN. 2007. Temporal occurrence of planktotrophic bivalve larvae identified morphologically and by single step nested multiplex PCR. Journal of Plankton Research. 29:423-436.
39. LUTTIKHUIZEN, P. C., J. DRENT, K. T. C. A. PEIJNENBURG, H. W. VAN DER VEER, and K. JOHANNESSON. 2012. Genetic architecture in a marine hybrid zone: comparing outlier detection and genomic clines analysis in the bivalve *Macoma balthica*. Molecular Ecology. 21:3048-3061.
40. LUTTIKHUIZEN, P. C., P. J. C. HONKOOOP, and J. DRENT. 2011. Intraspecific egg size variation and sperm limitation in the broadcast spawning bivalve *Macoma balthica*. Journal of Experimental Marine Biology and Ecology. 396:156-161.
41. MARRIAGE, L. D. 1954. The bay clams of Oregon. Contribution No. 20. Fish Commission of Oregon, s.l.
42. MEEHAN, B. W. 1985. Genetic comparison of *Macoma balthica* (Bivalvia, Telinidae) from the eastern and western north Atlantic Ocean. Marine Ecology Progress Series. 22:69-76.
43. NEWELL, R. 1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. Proceedings of the Zoological Society of London. 144:25-45.
44. OLDROYD, I. S. 1924. Marine shells of Puget Sound and vicinity. University of Washington Press, Seattle.
45. PHILIPPART, C. J. M., H. M. VAN AKEN, J. J. BEUKEMA, O. G. BOS, G. C. CADEE, and R. DEKKER. 2003. Climate-related changes in recruitment of the bivalve *Macoma balthica*. Limnology and Oceanography. 48:2171-2185.
46. PIERSMA, T., A. KOOLHAAS, A. DEKINGA, J. J. BEUKEMA, R. DEKKER, and K. ESSINK. 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. Journal of Applied Ecology. 38:976-990.
47. QUAYLE, D. B. 1970. The intertidal bivalves of British Columbia. British Columbia Provincial Museum, Victoria, BC, Canada.
48. RAE, J. G. 1979. Population dynamics of two sympatric species of *Macoma* (Mollusca, Bivalvia). Veliger. 21:384-399.
49. SAUNIER, A., P. GARCIA, V. BECQUET, N. MARSAUD, F. ESCUDIE, and E. PANTE. 2014. Mitochondrial genomes of the Baltic clam *Macoma balthica* (Bivalvia: Tellinidae): setting the stage for studying mito-nuclear incompatibilities. BMC Evolutionary Biology. 14:259.
50. SCOTT, P. V., and J. A. BLAKE. 1998. The Mollusca Part 1: the Aplacophora, Polyplacophora, Scaphopoda, Bivalvia and Cephalopoda. Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and the Western Santa Barbara Channel, vol. 8. Santa Barbara Museum of Natural History, Santa Barbara, CA.
51. SEITZ, R. D. 2011. Gradient effects on structuring of soft-bottom benthic infauna: *Macoma balthica* and predation, recruitment, and food availability. Journal of Experimental Marine Biology and Ecology. 409:114-122.
52. SWENNEN, C. 1969. Crawling-tracks of trematode infected *Macoma balthica* (L.). Netherlands Journal of Sea Research. 4:376-379.

53. THOMPSON, J. K., and F. H. NICHOLS. 1988. Food availability controls seasonal cycle of growth in *Macoma balthica* (L.) in San Francisco Bay, California. *Journal of Experimental Marine Biology and Ecology*. 116:43-61.
54. TORNROOS, A., M. C. NORDSTROM, K. AARNIO, and E. BONSDORFF. 2015. Environmental context and trophic trait plasticity in a key species, the tellinid clam *Macoma balthica* L. *Journal of Experimental Marine Biology and Ecology*. 472:32-40.
55. VAINOLA, R. 2003. Repeated trans-Arctic invasions in littoral bivalves: molecular zoogeography of the *Macoma balthica* complex. *Marine Biology*. 143:935-946.
56. VAN COLEN, C., E. DEBUSSCHERE, U. BRAECKMAN, D. VAN GANSBEKE, and M. VINCX. 2012. The early life history of the clam *Macoma balthica* in a high CO₂ world. *Plos One*. 7.
57. VASSALLO, M. T. 1969. The ecology of *Macoma inconspicua* (Broderip and Sowerby, 1829) in central San Francisco Bay. Part 1. The vertical distribution of the *Macoma* community. *Veliger*. 11:223-234.
58. —. 1971. The ecology of *Macoma inconspicua* (Broderip & Sowerby, 1829) in central San Francisco Bay. Part 2. Stratification of the *Macoma* community within the substrate. *Veliger*. 13:279-285.
59. YONGE, C. M. 1949. On the structure and adaptations of the Tellinacea, deposit-feeding Eulamelibranchia. *Transactions of the Royal Society of London, Series B*. 234:29-76.

Updated 2015

T.C. Hiebert and K. Meyer

Macoma inquinata

Irus clam

Phylum: Mollusca
Class: Bivalvia; Heterodonta
Order: Veneroida
Family: Tellinidae

Taxonomy: *Macoma balthica*, *M. nasuta* and *M. inquinata* were all originally described as members of the genus *Tellina*. *Tellina inquinata* and *T. irus*, initially described as different species (the former with eastern Pacific distribution, the latter with western), were synonymized in the genus *Heteromacoma*. Later, this synonymization was reversed based on characters of shell morphology and *Macoma inquinata* (previously, and confusingly, called *M. irus*) was deemed a member of the genus *Macoma*, with an eastern Pacific distribution while *H. irus*, remained a *Heteromacoma*, with a the western Pacific (see Keen 1962; Coan 1971). Thus, known synonyms for *M. inquinata* include *T. inquinata* as well as *M. irus*. Subspecific designations are also sometimes seen (e.g. *Macoma heteromacoma inquinata*, Kabat and O'Foighil 1987). *Macoma inquinata* is the name almost exclusively used in current intertidal guides (e.g. Coan and Valentich-Scott 2007).

Description

Size: Individuals up to 55 mm in length (Coan 1971). The illustrated specimen (Fig. 1) is 44 mm in length, 35 mm in height, and 18 mm in diameter.

Color: Shell is dull white, with a dark and opaque periostracum (not shiny) (see Fig. 294, Kozloff 1993). Interior shell is porcellanous white and feebly polished (Dunnill and Ellis 1969). Siphons are only barely yellowish in color (Kozloff 1993).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Among the bivalves, the Heterodonta are characterized by **ctenidia** (or gills) that are eulamellibranchiate, fused mantle margins and the presence of long **siphons**. Veneroid bivalves have well-developed hinge teeth and members of the family Tellinidae have short lateral hinge teeth (when present – see **Possible Misidentifications**), shells with

external striations or ribs, and deep pallial sinuses (Coan and Valentich-Scott 2007). When holding closed shell in both hands with the hinged area up and the ligaments toward you, the right valve is in the right hand (Fig. 4) (Keen and Coan 1974).

Body:

Color:

Interior: Ligament is long, strong, narrow, and prominent (Figs. 1, 4). It is not seated on a nymph, but is entirely external (Tellinidae, Coan and Valentich-Scott 2007).

Exterior:

Byssus:

Gills:

Shell: Shape ovate or subovate, but not circular. Posterior end is narrower and less rounded than anterior end. Shell is heavy, not fragile and inflated, with subcentral umbones (Fig. 1). Occasionally, there is a slight gape and flex to right on the posterior end (Dunnill and Ellis 1969).

Interior: Pallial line is not detached from the anterior ventral end of pallial sinus (Fig. 2) and is longer in the left valve (Fig. 3). The pallial sinus reaches almost to the anterior adductor scar, or just to its base in the left valve (Fig. 3) (Coan 1971). The pallial sinuses are similar in the two valves (e.g. compare to *M. nasuta*, this guide).

Exterior: External shell bears conspicuous concentric sculptural undulations (Fig. 1).

Hinge: Hinge with ligament is entirely external and no lateral teeth (*Macoma*, Coan and Valentich-Scott 2007). Hinge area includes two cardinal teeth in each valve, but no lateral teeth (Fig. 5).

Eyes:

Foot:

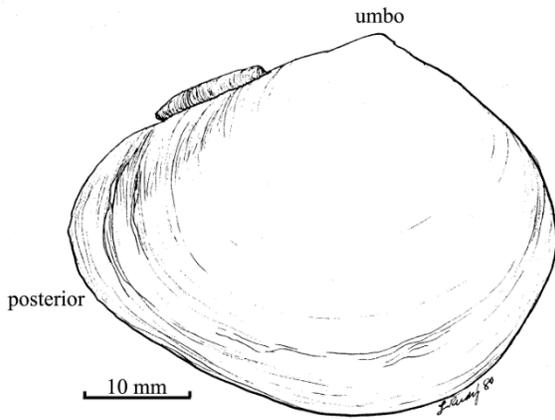
Siphons: The inhalant and exhalant siphons are completely separate (Fig. 1a) (Quayle 1970; Kozloff 1993).

Burrow:

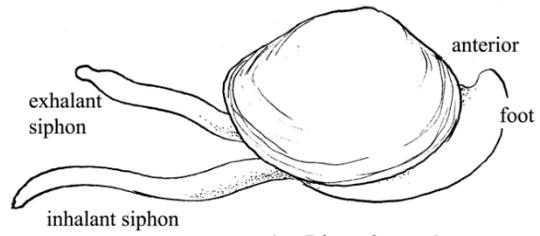
Possible Misidentifications

Tellinids can be distinguished from other small or young bay clams (i.e.

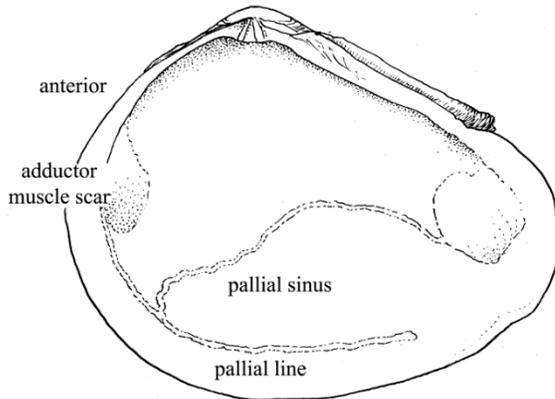
Macoma inquinata



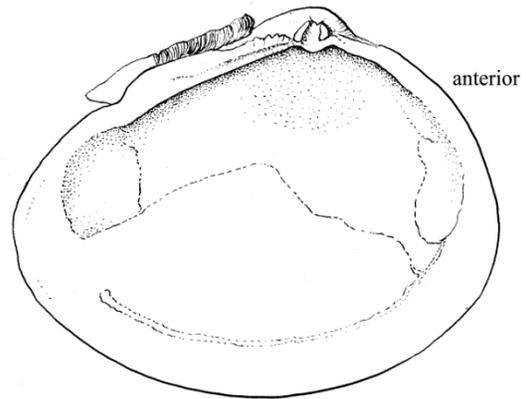
1. *Macoma inquinata*, right valve (L:44mm,D:18mm, H:35mm) x2: shell subovate, posterior narrow; valves equal, inflated; umbones subcentral; color dull white.



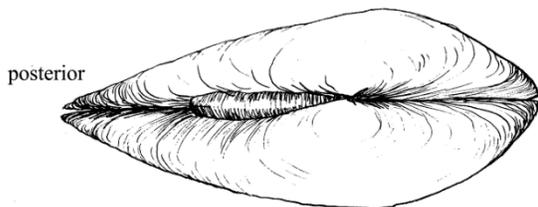
1a. Live clam x1: siphons separate.



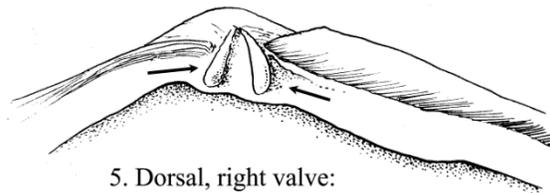
2. Interior, right valve: pallial sinus reaches almost to base of anterior adductor muscle scar.



3. Interior, left valve: pallial sinus as in right valve.



4. (Dorsal view): ligament external; valves slightly bent right posteriorly.



5. Dorsal, right valve: two cardinal teeth in each valve, no lateral teeth.

Mactridae: *Tresus*; Veneridae: *Protothaca*, *Saxidomus*; Myidae: *Mya*, *Cryptomya*) an external ligament, an ovate shell, an inconspicuous nymph (or supporting projection for the external ligament), sometimes reddish hue and lateral teeth as well as a shell with ribs or striations (no radial pattern) and shells that never gape. Lateral teeth may or may not be present in the Tellinidae (Coan 1971). Myids have a hinge with a spoon-shaped chondrophore (left valve) and a projecting tooth (right valve) (see *Mya arenaria*, this guide). Venerids have three cardinal teeth in each valve. Mactrids have an internal ligament, A-shaped cardinal teeth, and gaping valves (Coan and Valentich-Scott 2007). The Tellinidae has around 16 species distributed between two genera locally – *Tellina* and *Macoma*. These genera can be differentiated by the hinge teeth, *Tellina* species have a hinge with lateral teeth, while *Macoma* species do not. *Macoma* species have shells that are also more rounded and inflated than *Tellina*, and are smooth, white, often chalky. They are characterized by having a ovate shell consisting of two equal valves, a dark and deciduous periostracum, two cardinal teeth, the absence of lateral teeth and a pallial sinus that is deeper on the left valve (Scott and Blake 1998; Arruda and Domaneschi 2005). *Macoma* species may also have a more northern geographic distribution while *Tellina* are elongate, relatively compressed, conspicuously sculptured, brightly colored, and usually warm water dwellers (Coan 1971). Eleven species in the infaunal genus *Macoma* (Luttikhuisen et al. 2012) are reported locally (although 30 have been identified in the northeastern Pacific, Dunnill and Ellis 1969), but only seven are described in local keys (e.g. Coan and Valentich-Scott 2007), the four most common species of *Macoma* in our area are *M. balthica*, *M. nasuta*, *M. inquinata*, and *M. secta* (Kabat and O’Foighil 1987).

Two species, *M. secta* and *M. indentata* have a posterior dorsal flange extending from posterior end to the external ligament, this is absent in other *Macoma* species. The former species is called the sand clam and has a quadrate and truncate posterior. The latter is elongate, has a pointed posterior, unique muscle scars, is relatively rare and small (to 2.5 cm) and

occurs from Trinidad, California southward. *Macoma secta*, also has a white shell, with a yellowish epidermis. Its right valve is more inflated than the left, and it can be large (to 120 mm) and is more common in clean sand, not in estuarine mud.

The morphology of the pallial sinus differentiates the other species. In species without a posterior dorsal flange, *M. acolasta* and *M. yoldiformis*, the anterior ventral edge of the pallial sinus is detached for a portion of the distance to the posterior adductor muscle scar. *Macoma acolasta* also has a rounded posterior, rather than pointed as in *M. yoldiformis* and is rare, sand-dwelling, and occurs from Bodega Bay, California, southward. *Macoma yoldiformis* is elongate, inflated, and thin, with the pallial sinus detached from the pallial line. Although the range of this clam is from Vancouver south to Baja California, it is not included in Puget Sound or British Columbia work (Dunnill and Ellis 1969). It can be found in silt in low intertidal of protected bays (Coan and Valentich-Scott 2007).

Macoma inquinata, *M. nasuta* and *M. balthica* (see descriptions in this guide) are all species with an anterior ventral edge of pallial sinus that is not detached and they tend to be larger (up to 110 mm) than *M. acolasta* or *M. yoldiformis* (less than 30 mm). *Macoma balthica* has a pinkish hue and a pallial sinus that ends $\frac{3}{4}$ of the way to anterior adductor muscle scar and is generally more oval than *M. nasuta* or *M. inquinata* (Kozloff 1993). In *M. inquinata*, the pallial sinus does not reach the ventral end of the anterior adductor muscle. *Macoma nasuta*, on the other hand, is not as round and heavy as *M. inquinata* and its pallial sinus reaches and joins the anterior adductor scar above its base (left valve). (Its right valve may be more like *M. inquinata*'s). Furthermore, its siphons are orange and its shell posterior is bent to the right (hence the name, bent-nose clam). *Macoma inquinata* can also bend slightly posteriorly, and may be confused with the thinner *M. nasuta*, without investigations of the other aforementioned features. In *M. balthica*, the pallial sinus that reaches to $\frac{1}{4}$ the anterior adductor muscle scar and the shell has a pinkish hue. (see Plate 422 for diagrams of these distinguishing characteristics in *Macoma*).

Macoma incongrua, generally a northern species, is the species closest to *M. inquinata*. It can be found intertidally to 36 meters. It is quite circular in outline, its pallial sinuses extend longer than in *M. inquinata*, and are different between its two valves, they are similar in *M. inquinata*'s valves. *Macoma incongrua* averages 30–40 mm in length (Dunnill and Ellis 1969).

(The following species may be present locally, but are not included in local dichotomous keys). *Macoma expansa*, is a rare, usually offshore species (to 50 mm) whose pallial sinuses are perpendicular to the pallial line. *Macoma elimata* is found only in 15–476 meters of water. *Macoma calcarea* is found from 35 meters and lower, from 37° north. Other northern subtidal species include the large *M. brota* and *M. lipara* (Dunnill and Ellis 1969).

Ecological Information

Range: Type locality is Columbia River, OR (Keen 1962). Known range includes Siberia, Aleutian Islands, British Columbia, south to Oregon and rare further south of Santa Barbara, California (Coan 1971).

Local Distribution: Distribution in many Oregon bays, particularly Tillamook, Coos, Siuslaw, Yaquina, and less common in Alsea, Nestucca, Netarts Bays (Hancock 1979).

Habitat: Usually in soft muddy sand (Dunnill and Ellis 1969; Kabat and O'Foighil 1987) and in protected areas. Individuals have also been found in coarse sand with shell hash, intertidal sand, and in fine sediment overlying flat rocks (British Columbia, Canada, Dunnill and Ellis 1969) as well as in eelgrass (Puget Sound, Washington, Kozloff 1974). Like other *Macoma* species (e.g., *M. nasuta*), *M. inquinata* individuals can be the subject of toxicity testing due to their uptake and retention of benthic compounds by deposit feeding. *Macoma inquinata* and other deposit feeders accumulate more aromatic hydrocarbons than suspension feeders (e.g., Roesijadi et al. 1978; Crecelius et al. 1980; Augenfeld et al. 1982).

Salinity: Individuals collected where salinity is 30.

Temperature: Cold to temperate waters. The presence of *M. inquinata* in the fossil record at Newport Bay, California during the late Pleistocene suggests historically cooler temperatures in that region (Powell 2001).

Tidal Level: Intertidal and subtidal (Kabat and O'Foighil 1987) to 48 m offshore (Coan 1971).

Associates: Often co-occurs with the congener, *M. nasuta* (South Slough of Coos Bay). Juvenile pea crabs, *Pinnixia littoralis*, can occur within the mantle cavity of *M. inquinata* and *M. nasuta* in Puget Sound, Washington (Haderlie and Abbott 1980).

Abundance: Common in bays (Kozloff 1993; Coan and Valentich-Scott 2007) and can be locally abundant (e.g. over 6 million at one small Coos Bay site, Gaumer 1978). *Macoma inquinata* was one of the dominant intertidal macrobenthic species in the Chukchi Sea (67–73°N, Wang et al. 2014).

Life-History Information

Reproduction: Separate sexes, gametes are discharged into the water through excurrent siphon. Gametogenesis for *M. nasuta* and *M. secta* is described by Rae (1978), with both species ripe with gametes in summer months (Tomales Bay, California). The reproduction and development has been described for the common congener, *M. balthica* (Caddy 1967, 1969; Lammens 1967), which spawns in spring and summer (Friday Harbor, Washington, Kabat and O'Foighil 1987).

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliate trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the "D" shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone (e.g. see *M. balthica*, Fig. 1, Caddy 1969). Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (Kabat and O'Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001). *Macoma balthica*, *M. nasuta* and *M. secta* are all

known to have free swimming veliger larvae (Marriage 1954; Rae 1978, 1979; Brink 2001).

Juvenile:

Longevity:

Growth Rate:

Food: Chiefly a deposit feeder (although also potentially a suspension feeder, see *M. nasuta* and *M. balthica*, this guide), feeding on surface bacteria and detritus with their siphons (Kabat and O'Foighil 1987). The feeding behavior of the congeners, *M. nasuta* and *M. inquinata* showed variation in response to water flow. Their inhalant siphons extended farther, allowing for deposit feeding over a larger area, when water flow was lower (Levinton 1991).

Predators: Shorebirds.

Bibliography

1. ARRUDA, E. P., and O. DOMANESCHI. 2005. New species of *Macoma* (Bivalvia: Tellinoidea: Tellinidae) from southeastern Brazil, and with description of its gross anatomy. *Zootaxa*:13-22.
2. AUGENFELD, J. M., J. W. ANDERSON, R. G. RILEY, and B. L. THOMAS. 1982. The fate of polyaromatic hydrocarbons in an intertidal sediment exposure system: Bioavailability to *Macoma inquinata* (Mollusca, Pelecypoda) and *Abarenicola pacifica* (Annelida, Polychaeta). *Marine Environmental Research*. 7:31-50.
3. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
4. CADDY, J. F. 1967. Maturation of gametes and spawning in *Macoma balthica* (L.). *Canadian Journal of Zoology*. 45:955-965.
5. —. 1969. Development of mantle organs, feeding, and locomotion in postlarval *Macoma balthica* (L.) (Lamellibranchiata). *Canadian Journal of Zoology*. 47:609-617.
6. COAN, E. V. 1971. The Northwest American Tellinidae. California Malacozoological Society, Berkeley.
7. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
8. CRECELIUS, E. A., J. M. AUGENFELD, D. L. WOODRUFF, and J. W. ANDERSON. 1980. Uptake of trace metals by the clam *Macoma inquinata* from clean and oil-contaminated detritus. *Bulletin of Environmental Contamination and Toxicology*. 25:337-344.
9. DUNNILL, R. M., and D. V. ELLIS. 1969. Recent species of the genus *Macoma* (Pelecypoda) in British Columbia. National Museum of Canada, National Historical Papers. 45:1-34.
10. GAUMER, T. F. 1978. Clam resources in a proposed Charleston boat basin expansion site. Information report 78-1. Oregon Department of Fish and Wildlife, Charleston, OR.
11. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
12. HANCOCK, D. R., T. F. GAUMER, G. B. WILLEKE, G. P. ROBERT, and J. FLYNN. 1979. Subtidal clam populations: distribution, abundance, and ecology. Oregon State University, Sea Grant College Program, Corvallis.
13. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
14. KEEN, A. M. 1962. Reinstatement of the specific name *Macoma inquinata* (Deshayes). *Veliger*. 4:161-161.
15. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
16. KOZLOFF, E. N. 1974. Seashore life of Puget Sound, the Strait of Georgia,

- and the San Juan Archipelago and adjacent regions. University of Washington Press, Seattle and London.
17. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 18. LAMMENS, J. J. 1967. Growth and reproduction in a tidal flat population of *Macoma balthica* (L.). Netherlands Journal of Sea Research. 3:315-382.
 19. LEVINTON, J. S. 1991. Variable feeding behavior in three species of *Macoma* (Bivalvia, Tellinacea) as a response to water flow and sediment transport. Marine Biology. 110:375-383.
 20. LUTTIKHUIZEN, P. C., J. DRENT, K. T. C. A. PEIJNENBURG, H. W. VAN DER VEER, and K. JOHANNESSON. 2012. Genetic architecture in a marine hybrid zone: comparing outlier detection and genomic clines analysis in the bivalve *Macoma balthica*. Molecular Ecology. 21:3048-3061.
 21. MARRIAGE, L. D. 1954. The bay clams of Oregon. Contribution No. 20. Fish Commission of Oregon, s.l.
 22. POWELL, C. L. 2001. Geologic and molluscan evidence for a previously misunderstood late Pleistocene, cool water, open coast terrace at Newport Bay, southern California. Veliger. 44:340-347.
 23. QUAYLE, D. B. 1970. The intertidal bivalves of British Columbia. British Columbia Provincial Museum, Victoria, BC, Canada.
 24. RAE, J. G. 1978. Reproduction in two sympatric species of *Macoma* (Bivalvia). Biological Bulletin. 155:207-219.
 25. —. 1979. Population dynamics of two sympatric species of *Macoma* (Mollusca, Bivalvia). Veliger. 21:384-399.
 26. ROESIJADI, G., J. W. ANDERSON, and J. W. BLAYLOCK. 1978. Uptake of hydrocarbons from marine sediments contaminated with Prudhoe Bay crude oil: influence of feeding type of test species and availability of polycyclic aromatic hydrocarbons. Journal of the Fisheries Research Board of Canada. 35:608-614.
 27. SCOTT, P. V., and J. A. BLAKE. 1998. The Mollusca Part 1: the Aplacophora, Polyplacophora, Scaphopoda, Bivalvia and Cephalopoda. Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel. Vol. 8. Santa Barbara Museum of Natural History, Santa Barbara, CA.
 28. WANG, J., H. LIN, X. HE, J. LIN, Y. HUANG, R. LI, C. ZHENG, F. ZHENG, and J. JIANG. 2014. Biodiversity and community structural characteristics of macrobenthos in the Chukchi Sea. Acta Oceanologica Sinica. 33:82-89.

Updated 2015

Macoma nasuta

The bent-nosed clam

Phylum: Mollusca
Class: Bivalvia; Heterodonta
Order: Veneroida
Family: Tellinidae

Taxonomy: Originally described in the genus *Tellina* by Conrad in 1837, additional synonyms include *Tellina tersa*, *Macoma kelseyi*, *M. jacalitosana*. Also subspecific designations (e.g. *Macoma Heteromacoma nasuta*, Kabat and O'Foighil 1987) are sometimes seen. However, *M. nasuta* is the name almost exclusively used in current intertidal guides (e.g. Coan and Valentich-Scott 2007).

Description

Size: Individuals range from 3 to 70 mm (Macginitie and Macginitie 1949; Kozloff 1993) and are seldom larger than 64 mm (Packard 1918). In Coos Bay, the largest individuals are approximately 58 mm, which would classify them as having a medium sized shell (see Keen and Coan 1974).

Color: Shell is white and chalky where eroded (see Fig. 293, Kozloff 1993) and has dark brown parchment periostracum, especially near lower edge and siphons on valves. Shell is often with black markings externally (Brusca and Brusca 1978) but there is no interior shell color (Keen and Coan 1974). Siphons can be orange (Kozloff 1993).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). Among the bivalves, the Heterodonta are characterized by **ctenidia** (or gills) that are eulamellibranchiate, fused mantle margins and the presence of long **siphons**. Veneroid bivalves have well-developed hinge teeth and members of the family Tellinidae have short lateral hinge teeth (when present – see **Possible Misidentifications**), shells with external striations or ribs, and deep pallial sinuses (Coan and Valentich-Scott 2007). When holding closed shell in both hands with the hinged area up and the ligaments toward you, the right valve is in the right hand (Fig. 4) (Keen and Coan 1974).

Body:

Color:

Interior: Ligament is entirely external and the is not supported by a nymph or projection dorsally (Fig. 5).

Exterior:

Byssus:

Gills:

Shell: Shells ovate (Fig. 1) and posterior portions of valves are distinctly bent to the right (“bent nose”, Kozloff 1993) (Fig. 4). The anterior end is rounded, and the posterior is wedge-shaped, or truncate (i.e. not flanged).

Interior: The pallial sinus of the right valves does not reach the anterior adductor scar (Fig. 3) (see Plate 422, Coan and Valentich-Scott 2007). The adductor and posterior muscle scars are similar in shape in both valves and overlaps, but sinus patterns differ. The pallial sinus of the left valve reaches the anterior adductor muscle scar, fuses and overlaps with it (Fig. 2) (Coan and Valentich-Scott 2007).

Exterior: Valve exterior is thin and smooth, but not polished. The shells are sometimes blackish and are thin, with fine radial lines.

Hinge: Hinge with ligament is entirely external and no lateral teeth (Fig. 5) (*Macoma*, Coan and Valentich-Scott 2007). Two cardinal hinge teeth are present on the right valve (Fig. 5) and one on the left valve (Fig. 2). The beak is central and slightly prominent (Fig. 5) (Packard 1918).

Eyes:

Foot:

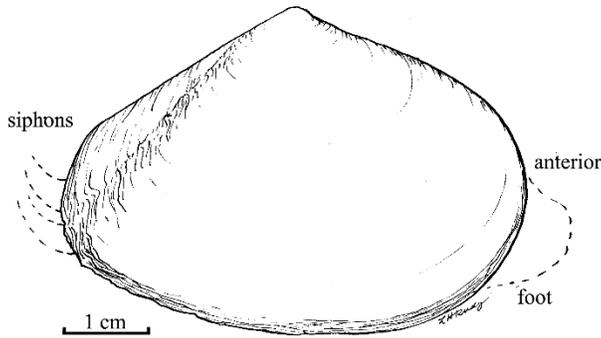
Siphons: The inhalant and exhalant siphons are completely separate and distinctly orange in color (Fig. 6) (Kozloff 1993).

Burrow: Clams burrow 10–20 cm within fine sediment, but these burrows are not permanent (Alexander et al. 1993; Volkenborn et al. 2012). For burrow schematic, see Fig. 8.10B, Zonneveld et al. 2014.

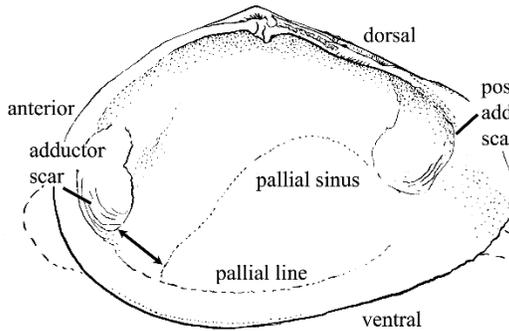
Possible Misidentifications

Tellinids can be distinguished from other small or young bay clams (i.e.

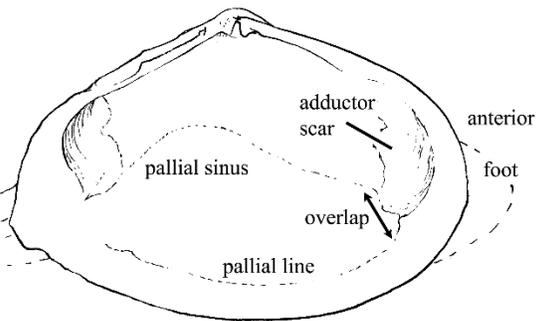
Macoma nasuta



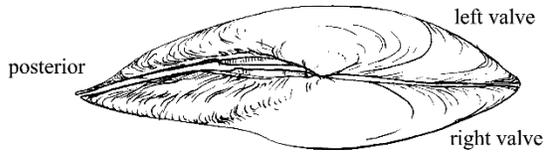
1. *Macoma nasuta*, external, right valve x1.63:
thin, white shell; bent right posteriorly; fine, radial lines; anterior rounded; posterior truncate.



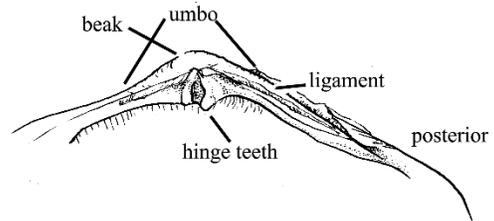
2. Interior, right valve:
pallial sinus doesn't reach anterior adductor scar;
muscle scars similar.



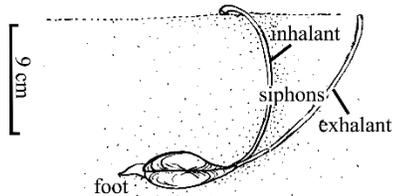
3. Interior, left valve:
pallial sinus overlaps anterior adductor scar.



4. Exterior (dorsal view):
posterior valves bent right.



5. Dorsal region, right valve:
two cardinal hinge teeth; hinge
external; no lateral teeth; ligament
dorsal, external, not on nymph; back
central, slightly prominent.



6. Clam burrowing x0.33
(MacGinitie, 1949).

Mactridae: *Tresus*; Veneridae: *Protothaca*, *Saxidomus*; Myidae: *Mya*, *Cryptomya*) an external ligament, an ovate shell, an inconspicuous nymph (or supporting projection for the external ligament), sometimes reddish hue and lateral teeth as well as a shell with ribs or striations (no radial pattern) and shells that never gape. Lateral teeth may or may not be present in the Tellinidae (Coan 1971). Myids have a hinge with a spoon-shaped chondrophore (left valve) and a projecting tooth (right valve) (see *Mya arenaria*, this guide). Venerids have three cardinal teeth in each valve. Mactrids have an internal ligament, A-shaped cardinal teeth, and gaping valves (Coan and Valentich-Scott 2007). The Tellinidae has around 16 species distributed between two genera locally – *Tellina* and *Macoma*. These genera can be differentiated by the hinge teeth, *Tellina* species have a hinge with lateral teeth, while *Macoma* species do not. *Macoma* species have shells that are also more rounded and inflated than *Tellina*, and are smooth, white, often chalky. They are characterized by having a ovate shell consisting of two equal valves, a dark and deciduous periostracum, two cardinal teeth, the absence of lateral teeth and a pallial sinus that is deeper on the left valve (Scott and Blake 1998; Arruda and Domaneschi 2005). *Macoma* species may also have a more northern geographic distribution while *Tellina* are elongate, relatively compressed, conspicuously sculptured, brightly colored, and usually warm water dwellers (Coan 1971). Eleven species in the infaunal genus *Macoma* (Luttikhuisen et al. 2012) are reported locally (although 30 have been identified in the northeastern Pacific, Dunnill and Ellis 1969), but only seven are described in local keys (e.g. Coan and Valentich-Scott 2007), the four most common species of *Macoma* in our area are *M. balthica*, *M. nasuta*, *M. inquinata*, and *M. secta* (Kabat and O’Foighil 1987).

Two species, *M. secta* and *M. indentata* have a posterior dorsal flange extending from posterior end to the external ligament, this is absent in other *Macoma* species. The former species is called the sand clam and has a quadrate and truncate posterior. The latter is elongate, has a pointed posterior, unique muscle scars, is relatively rare and small (to 2.5 cm) and

occurs from Trinidad, California southward. *Macoma secta*, also has a white shell, with a yellowish epidermis. Its right valve is more inflated than the left, and it can be large (to 120 mm) and is more common in clean sand, not in estuarine mud.

The morphology of the pallial sinus differentiates the other species. In species without a posterior dorsal flange, *M. acolasta* and *M. yoldiformis*, the anterior ventral edge of the pallial sinus is detached for a portion of the distance to the posterior adductor muscle scar. *Macoma acolasta* also has a rounded posterior, rather than pointed as in *M. yoldiformis* and is rare, sand-dwelling, and occurs from Bodega Bay, California, southward. *Macoma yoldiformis* is elongate, inflated, and thin, with the pallial sinus detached from the pallial line. Although the range of this clam is from Vancouver south to Baja California, it is not included in Puget Sound or British Columbia work (Dunnill and Ellis 1969). It can be found in silt in low intertidal of protected bays (Coan and Valentich-Scott 2007).

Macoma inquinata, *M. nasuta* and *M. balthica* (see descriptions in this guide) are all species with an anterior ventral edge of pallial sinus that is not detached and they tend to be larger (up to 110 mm) than *M. acolasta* or *M. yoldiformis* (less than 30 mm). *Macoma balthica* has a pinkish hue and a pallial sinus that ends $\frac{3}{4}$ of the way to anterior adductor muscle scar and is generally more oval than *M. nasuta* or *M. inquinata* (Kozloff 1993). *Macoma inquinata* is a common mud clam, with slightly inflated but not dramatically bent valves. In *M. inquinata*, the pallial sinus does not reach the ventral end of the anterior adductor muscle and the shell is chalky white with a fibrous olive green periostracum. *Macoma nasuta*, on the other hand, is not as round and heavy as *M. inquinata* and its pallial sinus reaches and joins the anterior adductor scar above its base (left valve). (Its right valve may be more like *M. inquinata*'s). Furthermore, its siphons are orange and its shell posterior is bent to the right (Fig. 4). *Macoma inquinata* can also bend slightly posteriorly, and may be confused with the thinner *M. nasuta*, without investigations of the other aforementioned features. In *M. balthica*, the pallial sinus that reaches to $\frac{1}{4}$ the anterior adductor muscle scar and the shell has a pinkish hue. (see Plate 422 for

diagrams of these distinguishing characteristics in *Macoma*). *Macoma balthica* and *M. inquinata* are generally smaller than *M. nasuta* (up to 5 cm) and the shell of *M. nasuta* is white in-side and out, with some dark periostracum.

(The following species may be present locally, but are not included in local dichotomous keys). *Macoma expansa*, is a rare, usually offshore species (to 50 mm) whose pallial sinuses are perpendicular to the pallial line. *Macoma elimata* is found only in 15–476 meters of water. *Macoma incongrua* is a generally northern species which can be found to 33°N latitude, intertidally to 36 meters. It has somewhat inflated valves, is usually 30–40 mm long, and almost round in outline (Dunnill and Ellis 1969). *Macoma calcarea* is found from 35 meters and lower, from 37° north. Other northern subtidal species include the large *M. brota* and *M. lipara* (Dunnill and Ellis 1969).

Ecological Information

Range: Type locality is Astoria, OR. Known range from Kodiak, Alaska to Baja California (Ricketts and Calvin 1971). Kodiak Island, Alaska to Cabo San Lucas, Baja California (Coan 1971; Rae 1978).

Local Distribution: Occurs locally, in bays as well as offshore below the surf zone (Coan and Valentich-Scott 2007).

Habitat: Preferred substrates include mud and muddy sand (Kabat and O'Foighil 1987), about 10–15 cm below the surface (Kozloff 1993). *Macoma nasuta* is very adaptable and can live in finer mud than other *Macoma* species, often in the extremely stale waters of small lagoons (Ricketts and Calvin 1971). Individuals also found in eelgrass beds (Kozloff 1974). A common deposit feeder is often used in sediment toxicity testing and biomarker responses (e.g., Boese et al. 1995; Werner et al. 2004; Cho et al. 2007; Amirbahman et al. 2013). Can burrow within muddy and silty sediment (i.e., a wide range of grain sizes, Alexander et al. 1993) up to 40 cm (Rae 1978). *Macoma nasuta* was the oldest intertidal species present at Queen Charlotte Islands in the fossil record (~13,210 C¹⁴ years) and was possibly the first species to colonize this area following the last glacial maximum. This early colonization was likely due to the tolerance of *M. nasuta* for low water temperature, high turbidity, low primary

productivity and low salinity. Following initial colonization, congeneric species, *M. calcarea* and *M. inquinata*, began to appear in the fossil record (Hetherington and Reid 2003).

Salinity: Adapted to a wide range of conditions and salinities.

Temperature: Temperate and cold waters. *Macoma nasuta* is not found in the Panamic province to the south.

Tidal Level: Intertidal and subtidal (Kabat and O'Foighil 1987). Most common in bays at mid-tide line (Coan and Valentich-Scott 2007). Also reported from low tide horizon to 137 meters, with decreasing numbers with depth (Rae 1978).

Associates: Occasionally infested with encysted larvae of the tapeworm *Anthobothrium* sp. (MacGinitie and MacGinitie 1949). Juvenile pea crabs, *Pinnixia littoralis*, can occur within the mantle cavity of *M. inquinata* and *M. nasuta* in Puget Sound, Washington (Haderlie and Abbott 1980). Also host to the commensal nemertean *Malacobdella macomae* (Haderlie and Abbott 1980; Kozloff 1991; Roe et al. 2007). Individuals also host the turbellarian, *Graffilla pugetensis* in the pericardial cavity (Schell 1989). While other bivalve species exhibited declined numbers associated with the exotic mussel, *Musculista senhousia*, *M. nasuta* populations were not negatively affected and, instead, increased in number (Mission Bay, San Diego, California, Crooks 2001). *Macoma nasuta* co-occurs with the congener, *M. inquinata*.

Abundance: On "every possible mud flat" (Ricketts and Calvin 1971) where it is often the most common clam (e.g., in Elkhorn Slough). Individuals are more abundant in habitats with more mud than sand (San Francisco Bay, California, Alexander et al. 1993). The most abundant bivalve collected in box cores (25 x 25 x 50 cm) from a coastal lagoon in Bodega Harbor, California (Everett 1994).

Life-History Information

Reproduction: Separate sexes, gametes are discharged into the water through excurrent siphon. Oregon spawning reportedly spring, early summer (Haderlie and Abbott 1980). Nuclear protein composition of sperm is described by Ausio (1988). Gametogenesis for *M. nasuta* and *M. secta* is described by Rae (1978) and reproduction and

development has been described for the common congener, *M. balthica* (Caddy 1967, 1969; Lammens 1967). Unspawned oocytes of *M. nasuta* were 48–57 µm in diameter. Individuals were observed to spawn most months of the year, with peak spawning from August to November (14°C, Rae 1978). Spawning occurs in a brief period of two days and sex ratios were 1:1, with no hermaphrodites seen in the populations (Tamales Bay, California, Rae 1978).

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliate trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the “D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone (e.g. see *M. balthica*, Fig. 1, Caddy 1969). Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (Kabat and O’Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001). *Macoma nasuta* and *M. secta* are known to have free swimming veliger larvae (MacGinitie and MacGinitie 1949; Marriage 1954; Rae 1978, 1979; Brink 2001).

Juvenile:

Longevity:

Growth Rate:

Food: Primarily a suspension feeder that also ingests detritus from mud surface with siphon, while discarding coarse, inedible material (MacGinitie and MacGinitie 1949; Kabat and O’Foighil 1987). In a comparison of individual growth on a diet of surface sediment versus detritus, the former supported better growth (Hylleberg and Gallucci 1975). When deposit feeding, *M. nasuta* sucks the top 1 mm of sediment by boring or rotating with the siphon tip (Fig. 6) and exhibits some selectivity in feeding (Hylleberg and Gallucci 1975; Gallucci and

Hylleberg 1976). Interstitial water amounted to only 4% of the total water ventilated (~0.2 ml per hour). Instead, the overlying water is primarily ventilated (~7.3 ml per hour, Winsor 1990). The average ventilation rate for *M. nasuta* was found to be lower than that of other filtering bivalves, suggesting that deposit feeding may be their dominant feeding mode (Specht and Lee 1989). *Macoma nasuta* was found to be actively deposit feeding 83% of the time (Volkenborg et al. 2012). (For irrigation patterns see Table 1, Volkenborn et al. 2012). The deposit feeding behavior of both *M. nasuta* and *M. inquinata* showed variation in response to water flow. Their inhalant siphons extended farther, allowing for deposit feeding over a larger area, when water flow was lower (Levinton 1991).

Predators: Small clams are fed upon by crabs (e.g., *Cancer productus*), seastars (e.g., *Pisaster* spp.), as well as the snail *Polinices lewisii* (Haderlie and Abbott 1980; Kozloff 1993) and shore birds.

Behavior: Usually situated within the mud with left valve down (MacGinitie and MacGinitie 1949; Kozloff 1993) and burrows 10–20 cm deep into the sediment (Volkenborn et al. 2012) with a burrowing rate that is highest in fine sand and muddy silt (Alexander et al. 1993).

Bibliography

1. ALEXANDER, R. R., R. J. STANTON, and J. R. DODD. 1993. Influence of sediment grain-size on the burrowing of bivalves: correlation with distribution and stratigraphic persistence of selected neogene clams. *Palaios*. 8:289-303.
2. AMIRBAHMAN, A., D. I. MASSEY, G. LOTUFO, N. STEENHAUT, L. E. BROWN, J. M. BIEDENBACH, and V. S. MAGAR. 2013. Assessment of mercury bioavailability to benthic macroinvertebrates using diffusive gradients in thin films (DGT). *Environmental Science-Processes & Impacts*. 15:2104-2114.
3. ARRUDA, E. P., and O. DOMANESCHI. 2005. New species of *Macoma* (Bivalvia: Tellinoidea: Tellinidae) from southeastern Brazil,

- and with description of its gross anatomy. *Zootaxa*:13-22.
4. AUSIO, J. 1988. An unusual cysteine-containing histone H1-like protein and 2 protamine-like proteins are the major nuclear proteins of the sperm of the bivalve mollusk *Macoma nasuta*. *Journal of Biological Chemistry*. 263:10141-10150.
 5. BOESE, B. L., M. WINSOR, H. LEE, S. ECHOLS, J. PELLETIER, and R. RANDALL. 1995. PCB congeners and hexachlorobenzene biota sediment accumulation factors for *Macoma nasuta* exposed to sediments with different total organic carbon contents. *Environmental Toxicology and Chemistry*. 14:303-310.
 6. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 7. BRUSCA, G. J., and R. C. BRUSCA. 1978. A naturalist's seashore guide. Mad River Press, Arcata, CA.
 8. CADDY, J. F. 1967. Maturation of gametes and spawning in *Macoma balthica* (L.). *Canadian Journal of Zoology*. 45:955-965.
 9. —. 1969. Development of mantle organs, feeding, and locomotion in postlarval *Macoma balthica* (L.) (Lamellibranchiata). *Canadian Journal of Zoology*. 47:609-617.
 10. CHO, Y., D. W. SMITHENRY, U. GHOSH, A. J. KENNEDY, R. N. MILLWARD, T. S. BRIDGES, and R. G. LUTHY. 2007. Field methods for amending marine sediment with activated carbon and assessing treatment effectiveness. *Marine Environmental Research*. 64:541-555.
 11. COAN, E. V. 1971. The Northwest American Tellinidae. California Malacozoological Society, Berkeley.
 12. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 13. CROOKS, J. A. 2001. Assessing invader roles within changing ecosystems: Historical and experimental perspectives on an exotic mussel in an urbanized lagoon. *Biological Invasions*. 3:23-36.
 14. DUNNILL, R. M., and D. V. ELLIS. 1969. Recent species of the genus *Macoma* (Pelecypoda) in British Columbia. National Museum of Canada, National Historical Papers. 45:1-34.
 15. EVERETT, R. A. 1994. Macroalgae in marine soft-sediment communities: effects on benthic faunal assemblages. *Journal of Experimental Marine Biology and Ecology*. 175:253-274.
 16. GALLUCCI, V. F., and J. HYLLEBERG. 1976. A quantification of some aspects of growth in the deposit feeding bivalve *Macoma nasuta*. *Veliger*. 19:59-67.
 17. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 18. HYLLEBERG, J., and V. F. GALLUCCI. 1975. Selectivity in feeding by deposit-feeding bivalve *Macoma nasuta*. *Marine Biology*. 32:167-178.
 19. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 20. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
 21. KOZLOFF, E. N. 1974. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago and adjacent regions. University of Washington Press, Seattle and London.
 22. —. 1991. *Malacobdella siliquae* sp. nov. and *Malacobdella macomae* sp. nov., commensal nemertean from bivalve mollusks on the Pacific Coast

- of North America. *Canadian Journal of Zoology*. 69:1612-1618.
23. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
 24. LAMMENS, J. J. 1967. Growth and reproduction in a tidal flat population of *Macoma balthica* (L.). *Netherlands Journal of Sea Research*. 3:315-382.
 25. LEVINTON, J. S. 1991. Variable feeding behavior in three species of *Macoma* (Bivalvia, Tellinacea) as a response to water flow and sediment transport. *Marine Biology*. 110:375-383.
 26. LUTTIKHUIZEN, P. C., J. DRENT, K. T. C. A. PEIJNENBURG, H. W. VAN DER VEER, and K. JOHANNESSON. 2012. Genetic architecture in a marine hybrid zone: comparing outlier detection and genomic clines analysis in the bivalve *Macoma balthica*. *Molecular Ecology*. 21:3048-3061.
 27. MACGINITIE, G. E., and N. MACGINITIE. 1949. Natural history of marine animals. McGraw-Hill Book Co., New York.
 28. MARRIAGE, L. D. 1954. The bay clams of Oregon. Contribution No. 20. Fish Commission of Oregon, s.l.
 29. PACKARD, E. L. 1918. Molluscan fauna from San Francisco Bay. *Zoology*. 14:199-452.
 30. PRUELL, R. J., N. I. RUBINSTEIN, B. K. TAPLIN, J. A. LIVOLSI, and R. D. BOWEN. 1993. Accumulation of polychlorinated organic contaminants from sediment by three benthic marine species. *Archives of Environmental Contamination and Toxicology*. 24:290-297.
 31. RAE, J. G. 1978. Reproduction in two sympatric species of *Macoma* (Bivalvia). *Biological Bulletin*. 155:207-219.
 32. —. 1979. Population dynamics of two sympatric species of *Macoma* (Mollusca, Bivalvia). *Veliger*. 21:384-399.
 33. RICKETTS, E. F., and J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 34. ROE, P., J. L. NORENBURG, and S. MASLAKOVA. 2007. Nemertea, p. 221-233. *In: Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 35. SCHELL, S. C. 1989. The structure of the nervous system of *Graffilla pugetensis*, a parasite in the pericardial cavity of the bent-nose clam, *Macoma nasuta*. *Journal of Parasitology*. 75:428-430.
 36. SCOTT, P. V., and J. A. BLAKE. 1998. The Mollusca Part 1: the Aplacophora, Polyplacophora, Scaphopoda, Bivalvia and Cephalopoda. Taxonomic atlas of the benthic fauna of the Santa Maria Basin and the Western Santa Barbara Channel. Vol. 8. Santa Barbara Museum of Natural History, Santa Barbara, CA.
 37. TURGEON, D. D., J. F. QUINN, A. E. BOGAN, E. V. COAN, F. G. HOCHBERG, W. G. LYONS, P. M. MIKKELSEN, R. J. NEVES, C. F. E. ROPER, G. ROSENBERG, B. ROTH, A. SCHELTEMA, F. G. THOMPSON, M. VECCHIONE, and J. D. WILLIAMS. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks. *American Fisheries Society Special Publication* 26. American Fisheries Society, Bethesda, MD.
 38. VOLKENBORN, N., C. MEILE, L. POLERECKY, C. A. PILDITCH, A. NORKKO, J. NORKKO, J. E. HEWITT, S. F. THRUSH, D. S. WETHEY, and S. A. WOODIN. 2012. Intermittent bioirrigation and oxygen dynamics in permeable sediments: An experimental and modeling study of three tellinid bivalves. *Journal of Marine Research*. 70:794-823.
 39. WERNER, I., S. J. TEH, S. DATTA, X. Q. LU, and T. M. YOUNG. 2004. Biomarker responses in *Macoma nasuta* (Bivalvia) exposed to sediments from northern San Francisco Bay. *Marine Environmental Research*. 58:299-304.
 40. WINSOR, M. H., B. L. BOESE, H. LEE, R. C. RANDALL, and D. T.

- SPECHT. 1990. Determination of the ventilation rates of interstitial and overlying water by the clam *Macoma nasuta*. *Environmental Toxicology and Chemistry*. 9:209-213.
41. ZONNEVELD, J., M. K. GINGRAS, C. A. HODGSON, L. P. MCHUGH, R. A. MYERS, J. A. SCHOENGUT, and B. WETTHUHN. 2014. Biotic segregation in an upper mesotidal dissipative ridge and runnel succession, West Salish Sea, Vancouver Island, British Columbia, p. 169-194. *In: Experimental approaches to understanding fossil organisms: lessons from the living*. Vol. 41. D. I. Hembree, B. F. Platt, and J. J. Smith (eds.).

Updated 2015

Leukoma staminea

Rock cockle, littleneck clam, hardshell clam or Pacific littleneck

Phylum: Mollusca
Class: Bivalva; Heterodonta
Order: Veneroida
Family: Veneridae

Taxonomy: Confusion surrounds the appropriate genus for this species. Many species were designated as *Protothaca* (or subspecies thereof, e.g., *Protothaca (Protothaca) staminea*, Kabat and O'Foighil 1987; Lazo 2004), based on shell sculpture, and are likely the same species. Many researchers have thus adopted the older designated name, *Leukoma* (e.g., Groesbeck et al. 2014) for the species described below (see (Coan and Valentich-Scott 2007). However, some local guides (e.g., Brink 2001) and several publications also use *Protothaca staminea*. Other synonyms include *Vererupsis staminea*, *Protothaca restoriationensis*, *Paphia staminea* and variations var. *runderata*, var. *orbella* (Deshayes; Carpenter).

Description

Size: Individuals 2–75 mm in length; average length is 25–50 mm (Ricketts and Calvin 1952; Kozloff 1993). Maximum length of 30.70 mm was reported for specimens collected in Prince William Sound, Alaska (Nickerson 1977).

Color: Overall color is variable. Young specimens often with brown markings like a brown checkerboard pattern on their shell (squares on each valve) (Kozloff 1993). Adults can be uniform brown, pinkish, or orange, with a white interior (Kozloff 1993)

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). The Veneroida is a large and diverse bivalve heterodont order that is characterized by well developed hinge teeth. There are 22 local families, and members of the Veneridae have three cardinal teeth on each valve (see Plate 396H, Coan and Valentich-Scott 2007) (Fig. 2).

Body: (see Fig. 299, Kozloff 1993).

Color:

Interior: The ligament is external and seated on a nymph. The mantle edge is composed of four tentacular folds, the fourth of which is large, glandular and comprised of mucocytes. There is also a large dorsal ridge, which contains mucopolysaccharides and protein-secreting cells (Hillman and Bennett 1979).

Exterior:

Byssus:

Gills:

Shell: The shell is very heavy, *L. staminea* is sometimes called the rock cockle because of its strong radiating ridges (Ricketts and Calvin 1952).

Interior: Shell interior is porcelaneous and the ventral margin is with fine crenulate sculpture (Fig. 2). The muscle scars are almost equal and the pallial line is broken by a deep pallial sinus (Fig. 2). The file-like structure of the inside ventral margin is a distinct feature of this species (Kozloff 1993).

Exterior: The shell shape is sub-oval and heavy. There are numerous, fine, radiating ribs as well as concentric ridges. The radial ribs are more conspicuous for individuals that nestle within rocks, i.e., those found in pholad borings (Coan and Carlton 1975). Specimens often have differing shell shapes based on their different habitats (Fraser and Smith 1928).

Hinge: There are three compressed cardinal teeth in the hinge area and no lateral teeth. The hinge plate is wide and set at an angle (Fig. 2).

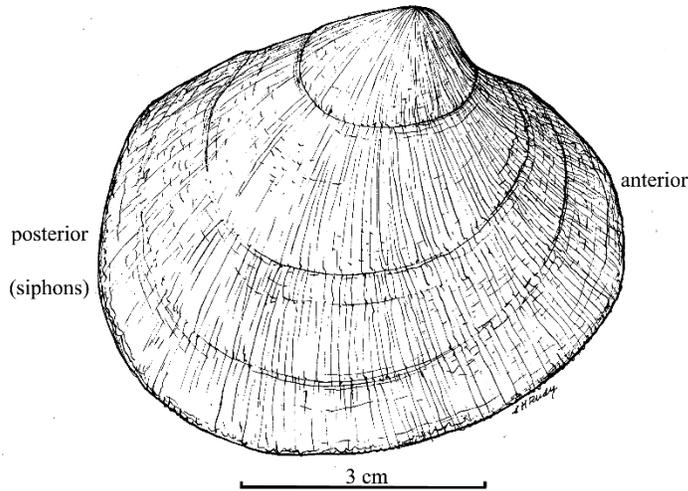
Eyes:

Foot:

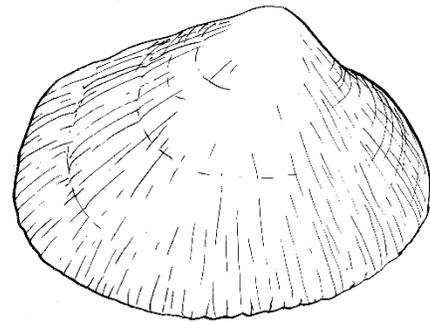
Siphons: The siphons are short and fused (Kozloff 1993).

Burrow: *Leukoma staminea* is a poor digger, and thus does not live in sediments that require frequent digging (e.g., those that shift) (Ricketts and Calvin 1952); prefers clay (Ricketts and Calvin 1952). Burrows are less than 20 cm deep (Ricketts and Calvin 1952). Not always buried at all (Dunham et al. 2006). Can move and reburrow using their foot

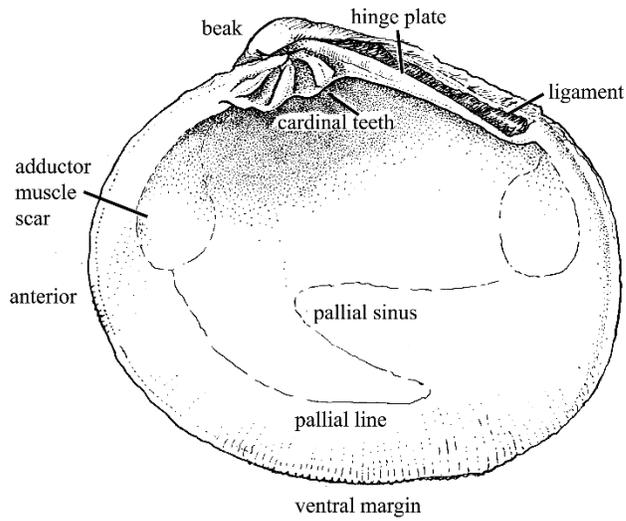
Leukoma staminea



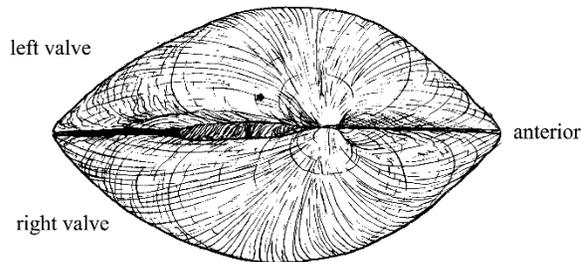
1. *Leukoma staminea*, exterior, right valve x1.5: many fine radiating ribs; concentric ridges also; shell suboval, heavy; posterior rounded.



1a. *Venerupis philippinarum* or *Ruditapes philippinarum* (Adams & Reeve, 1850) x1.5: introduced clam; elongate, strong radial ribs.



2. Interior, right valve: chalky, parcelaneous; ventral margin crenulate; muscle scars subequal; pallial sinus deep; hinge plate angled, ligament external, on nymph; three cardinal teeth, no lateral teeth.



3. (Dorsal view)

(Shaw 1986). Semi-infaunal to 10 cm in coarse sediment; burrowing rate depends on the sediment size, with faster burrowing in finer sediment (Alexander et al. 1993).

Possible Misidentifications

Veneroida is a large bivalve order, characterized by well-developed hinge teeth, including most heterodonts. The family Veneridae is characterized by a hinge without lateral teeth, ligament that is entirely external, radial ribs on shell exterior, and three cardinal teeth on each shell valve. There are 12–16 species reported locally in this family within the genera *Nutricola*, *Saxidomus*, and *Leukoma*, with two species in each, and *Gemma gemma*, *Irusella lamellifera*, *Tivela stultorum*, *Venerupis philippinarum*, *Mercenaria mercenaria*, *Callithaca tenerrima*, each with a single species represented locally.

Nutricola species are small, with shells usually less than 10 mm in length. *Gemma gemma* also has a small shell, but it is triangular in shape compared to *Nutricola* species with elongate or oval shells. *Tivela stultorum* also has a triangular shell, but individuals are larger than *G. gemma* and have a smooth shell surface with shiny periostracum. *Nutricola tantilla* has a shell that is white in color and siphons that are fused (or nearly so) at the tips. *Nutricola confusa* has a shell that is purple in color, siphons that bear a conspicuous cleft as well as conspicuous anterior lateral teeth, which are weak in *N. tantilla*.

The remaining species have shells larger than 10 mm in length. Some species have shell sculpturing that is dominated by commarginal ribs with fine radial ridges and others have shells that have radial ridges with inconspicuous, or not predominating, commarginal ribs. Of those in the former category, *I. lamellifera* has widely spaced commarginal lamellae and a shell that is short compared to *M. mercenaria* and *C. tenerrima*. The two latter species have elongated shells, no anterior lateral teeth and valves that do not gape. *Saxidomus* species also have an elongate shell, when compared to *I. lamellifera*, but they possess anterior lateral teeth and valves that are separated by a narrow gape, posteriorly. *Saxidomus nuttalli* and *S. giganteus* can be differentiated as the former species has a elongate and thinner

shell as well as a narrow escutcheon (not present in *S. giganteus*). The shell sculpturing in *S. giganteus* also appears smooth as the commarginal ribs are thin, low and tightly spaced, while the opposite is true for *S. nuttalli*.

The venerid species without predominately commarginal ribs include *Ruditapes philippinarum* (Adams & Reeve, 1850) (called *Venerupis philippinarum* in the most recent Light and Smith manual) and members of the genus *Leukoma*. *Leukoma* species differ from *R. philippinarum* by having an inner ventral margin that is not smooth (i.e., inner margin crenulated), a ligament that is not prominent and fused siphons. *Leukoma staminea* has shell sculpturing that is dominated by numerous radiating ribs, with faint commarginal ridges and the opposite is true for its congener (i.e., dominant radiating and commarginal ridges).

A closely related Venerid, *R. philippinarum* (Fig. 1a), has been introduced from Japan, and is common in mud of bays (Coan and Carlton 1975). It is elongate, oval, and has a prominently elevated ligament. Its radial ribs are quite strong and its color pattern distinctive. Its internal ventral margin is smooth, not crenulate, and its pallial sinus only moderately deep. Its internal color is yellowish with a purple stain. It lives at slightly higher elevations than does *L. staminea* and can grow to 50 mm in length (Washington, Haderlie 1980). Other bay clams of the same size and habitat as *L. staminea* lack both its radial and concentric sculpture.

Ecological Information

Range: Type locality is California (see Orr et al. 2013). Known range extends from the Aleutian Islands in Alaska to the Socorro Islands, Mexico. Previously known varieties of this species were divided into those north of San Francisco: var. *runderata* (on beaches) and var. *orbella* (in pholad borings). Northern limit is Prince William Sound, Alaska (Feder et al. 1979).

Local Distribution: *Leukoma staminea* is a common clam in most of the larger Northwest estuaries and bays, and around rocky ocean outcroppings.

Habitat: Occurs in coarse sand as well as fine gravel with mud, stones, or shell (Kozloff 1974); seldom found in fine, pure sand

(Fraser and Smith 1928). As it is a poor digger, *L. staminea* does not do well in shifting sand, but prefers packed mud, clayey gravel (Ricketts and Calvin 1971). Individuals usually found 3–8 cm below surface, or nestling into sand, rocks, and empty pholad holes (Coan and Valentich-Scott 2007). Both *L. staminea* and *Mytilus edulis* co-occur in Auke Bay, Alaska where their survival is negatively effected by burial depth (as little as 6 cm) and duration by bark chips from a log transferring facility (Freese and O'Clair 1987). A bioindicator species (e.g., Swartz et al. 1979; copper and copper-binding proteins Roesijadi 1980), *Leukoma staminea* survival and growth was also negatively effected by oil from the *Exxon Valdez* oil spill at least 5–6 years following the spill (Fukuyama et al. 2000; Fukuyama et al. 2014). Aside from the negative effect of hydrocarbon accumulation within clam tissues (see Thomas et al. 2007), Fukuyama et al. (2014) suggest that the removal of fine sediment associated with oil spill cleanup had a negative impact on *L. staminea* populations. However, when tested for the accumulation of hydrocarbons from crude oil, *L. staminea* (a suspension feeder) showed less uptake than deposit feeders (e.g., *Macoma inquinata* and *Phascolosoma agassizii*, Roesijadi et al. 1978). Interestingly, *L. staminea* individuals were also more likely to be preyed upon by *Cancer magister* in oiled habitats (Pearson et al. 1981). “Clam gardens”, created adjacent to intertidal rock walls constructed by human populations in the Holocene, have four times as many *S. giganteus* and twice as many *L. staminea* individuals as non-walled beaches, and transplanted juveniles of the latter species also grow faster (1.7 times faster) in clam gardens (Groesbeck et al. 2014). Individuals may be both infaunal when found in mud and muddy sand or epifaunal among gravel, the latter habitat yielding the most damaged shells (Lazo 2004). Unlike the co-occurring bivalve, *Macoma balthica*, populations of *L. staminea* in Puget Sound, Washington showed genetic heterogeneity reflecting and potentially caused by the hydrology of the Puget Sound (Parker et al. 2003).

Salinity: Collected at salinities of 30.

Temperature:

Tidal Level: Intertidal and subtidal (Hancock et al. 1979); upper 20 cm of cobble, sand and mud (Kabat and O'Foighil 1987). Occurs from

below half tide to lowest tideline (Puget Sound, Washington, Kozloff 1974). A range of +1.52 to -0.76 m was reported for individuals in Prince William Sound, Alaska (Nickerson 1977).

Associates: Often found with the cockle, *Clinocardium nuttallii*, and particularly with the butter clam, *Saxidomus giganteus* (Nickerson 1977). Often bored by drilling gastropods (Haderlie 1980). The majority (~70%) of *L. staminea* individuals collected from Cooper's Cove, British Columbia were infested with cysts from an apicomplexan parasite that were 20–150 µm in diameter (Desser and Bower 1997). *Leukoma staminea* and *S. giganteus* co-occur on Kiket Island, Washington, where the greatest diversity and richness of other marine invertebrates are found (Houghton 1977). Co-occurs with other clams (e.g., *Tresus capax* and *T. nuttallii*, Gillispie and Bourne 2004; *Sanguinolaria nuttallii*, Peterson and Andre 1980), but the presence of these species does not seem to effect *L. staminea* abundance (Peterson and Andre 1980). It has been suggested that the non-indigenous manila clam, *Venerupis philippinarum* is outcompeting and replacing *L. staminea* in some habitats (British Columbia, Canada, Bendell 2014).

Abundance: *Leukoma staminea* is common; the most abundant clam of the lower intertidal in Puget Sound, Washington (Kozloff 1974). In a Coos Bay estimate (of the genus *Protothaca*) from 1975, Hancock et al., estimated there were 843,000 clams weighting 32.6 metric tons (Hancock et al. 1979). Also common in Tillamook Bay, but the density of individuals is light in Alsea, Siuslaw, and Netarts estuaries (Hancock et al. 1979). Can be very abundant with several individuals in one shovel full, and can even be raked from just under the sediment surface (Kozloff 1993). Individuals sometimes even on top of one another: “2 to 3 shovels full will yield enough clams to feed several hungry people” (Ricketts and Calvin 1952). In British Columbia beaches, assessed in 1993, *L. staminea* density was ranged from 0 to 180 individuals/m² (Gillispie and Bourne 2004). In 2006, low densities were reported (presumably due to over harvest) in British Columbia, Canada (up to 7 individuals/m², Dunham et al. 2006). Estimates of the total population of *L. staminea* at Chugachik Island, Alaska were determined for 1992,

1995, and 1996 as 7.2, 3.3, and 5.5 million clams, respectively. Of this total, 136,000, 65,000, and 115,000 kg were harvested commercially (Bechtol and Gustafson 1998).

Life-History Information

Reproduction: Dioecious (separate sexes), but some hermaphroditism occurs (Fraser and Smith 1928; Kabat and O'Foighil 1987). Spawning in Oregon occurs from April through August (Robinson and Breese 1982) and in February–March (Puget Sound, Washington and Sydney, British Columbia, Canada, Ricketts and Calvin 1952). Spawning has also been reported from April to September for the Strait of Georgia (Quayle 1943 in Kabat and O'Foighil 1987; Shaw 1986) and in January in Vancouver BC (Fraser 1929). Quayle (1943) reported that females may spawn several times during a season, while males release all gametes at once; while Feder et al. (1979) found females spawn from June–September and males from June–January in Prince William Sound, Alaska. Spawning in response to algal blooms has been reported for this species as well as *Saxidomus giganteus* (Robinson and Breese 1982). Gametes discharged through the siphon during spawning (Shaw 1986).

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a D-stage or straight-hinge veliger due to the “D” shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone (see Fig. 1, Caddy 1969). Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig. 1, Caddy 1969; Kabat and O'Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001). Free-swimming (Brink 2001) veliger larvae of *L. staminea* are found in the plankton after

spawning from April to September through October (Strait of Georgia, Quayle 1943 in Kabat and O'Foighil 1987) and February in Vancouver, British Columbia (Kabat and O'Foighil 1987), and from April through October (Broughton Archipelago, British Columbia, Dunham et al. 2006). Ideal conditions for rearing larvae are 10–15°C at salinities of 32. Larvae can survive at slightly higher temperatures (e.g., 20°C) at the same salinity but higher temperatures and low salinity (e.g., 27) are lethal (Phibbs 1971). Trochophore larvae are 60–80 µm at 12 hours, straight-hinge veligers at 24 hours. Larvae have a ciliated velum and are 150 µm in length after 1 week, and an umbo when they are 260–280 µm in length at roughly 2 weeks. The total pelagic duration of *L. staminea* is 3 to 4 wks (Shaw 1986). At metamorphosis, larvae are 260–280 µm in length (Gillespie and Kronlund 199).

Juvenile: Gonads are apparent when juveniles are 1 mm in length, but sexes cannot be differentiated until they are 15–30 mm in length, a size reached by 2–3 years (Shaw 1986; Kabat and O'Foighil 1987). Individuals begin spawning after two years.

Longevity: A few individuals over seven years old were observed by Schmidt and Warne (1969). Mortality is greatest before sexual maturity (60%) and in old age (Schmidt and Warne 1969). Few clams are older than ten years (Fraser and Smith 1928), with a maximum age up to 13 (Shaw 1986) or 15 years (Nickerson 1977).

Growth Rate: Growth rate and age are determined by examination of rings caused by reduced growth in winter or different growth rates in different localities (but see Berta 1976). Growth is often slow in early years on exposed beaches, due to movement, storms, etc. and becomes more rapid in later years (the opposite may be true for individuals in protected sites). By the end of second year, specimens are 25 mm in length, and the third year, they are 35 mm (Fraser and Smith 1928). Clams were 47–54, 40–45 mm in length were estimated to be 6–8 and 3–7 years old at three sites in the Broughton Archipelago, British Columbia, Canada, respectively (Dunham et al. 2006). At three British Columbia beaches measured in 1993, individuals 25–50 mm in length were 3–7 years old, 30–64 mm were 3–9 years, and 29–46 were 3–8 years old; with individuals

reaching 38 mm in length at four years of age (Gillispie and Bourne 2004). Legal catch size is 38 mm in length, which occurs when individuals are approximately 4–5 years old (Bechtol and Gustafson 1998; Gillispie and Bourne 2004). Growth rate decreases as intraspecific density increases (Peterson 1982). A length of 30 mm was achieved in 8 years (see also Fig. 4, Shaw 1986).

Food: A suspension feeder, with short siphons that necessitate feeding close to sediment surface. The ingestion and concentration of toxic algae (e.g., from the genera *Alexandrium*, *Gymnodinium*, *Pyrodinium*, Smolowitz and Doucette 1995) leads to paralytic shellfish poisoning, rendering the clams dangerous for human consumption (Ricketts and Calvin 1952).

Predators: Adults are often preyed upon by birds (e.g., diving ducks, Fukuyama et al. 2000), terrestrial animals (Fukuyama et al. 2000), and drilling gastropods (e.g., *Polinices lewisii*, Peitso et al. 1993; Grey et al. 2007), sea stars, fish (siphon nipping, Peterson and Quammen 1982), and sea otters (Feder et al. 1979). Crabs, *Cancer productus*, forage for clams in areas where they are most dense (Boulding and Hay 1984; Boulding and Labarbera 1986), the European green crab, *Carcinus maenas* (Curtis et al. 2012), *Cancer magister* (Pearson et al. 1981; Juanes and Hartwick 1990), and *Cancer anthonyi* (Peterson 1983). *Leukoma staminea* is also an intermediate host to the “sporocysts of a Coccidia-like Apicomplexa” (see **Associates**, Desser and Bower 1997). Larvae are prey to planktonic predators and other suspension feeders. Common in coastal middens (~3-9 ka, Takesue and Geen 2004). A commercially harvested species, and populations were dramatically depleted in 1931 (Ricketts and Calvin 1952; Shaw 1986). A harvest as high as over 100,000 kg was reported in 1975 (Broughton Archipelago, British Columbia, Canada, Dunham et al. 2006). (see Bechtol and Gustafson 1998 for commercial summary). After this peak in 1975, landings decreased dramatically.

Behavior: A poor digger, *L. staminea* does not burrow vertically; the siphons and foot are short. Thus individuals remain close to surface of substrate and burrows easily horizontally (personal communication H. Van Veldhuizen).

Bibliography

1. ALEXANDER, R. R., R. J. STANTON, and J. R. DODD. 1993. Influence of sediment grain-size on the burrowing of bivalves: correlation with distribution and stratigraphic persistence of selected neogene clams. *Palaios*. 8:289-303.
2. BECHTOL, W. R., and R. L. GUSTAFSON. 1998. Abundance, recruitment, and mortality of Pacific littleneck clams *Protothaca staminea* at Chugachik Island, Alaska. *Journal of Shellfish Research*. 17:1003-1008.
3. BENDELL, L. I. 2014. Evidence for declines in the native *Leukoma staminea* as a result of the intentional introduction of the non-native *Venerupis philippinarum* in coastal British Columbia, Canada. *Estuaries and Coasts*. 37:369-380.
4. BERTA, A. 1976. An investigation of individual growth and possible age relationships in a population of *Protothaca staminea* (Mollusca: Pelecypoda). *Paleobios*. 21:1-26.
5. BOULDING, E. G., and T. K. HAY. 1984. Crab response to prey density can result in density-dependent mortality of clams. *Canadian Journal of Fisheries and Aquatic Sciences*. 41:521-525.
6. BOULDING, E. G., and M. LABARBERA. 1986. Fatigue damage: repeated loading enables crabs to open larger bivalves. *Biological Bulletin*. 171:538-547.
7. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
8. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
9. CURTIS, D. L., L. SAUCHYN, L. KEDDY, T. W. THERRIAULT, and C. M. PEARCE. 2012. Prey preferences and relative predation rates of adult European green crabs (*Carcinus*

- maenas*) on various bivalve species in British Columbia, Canada. Canadian Technical Report of Fisheries and Aquatic Sciences. 3014:1-14,III.
10. DESSER, S. S., and S. M. BOWER. 1997. The distribution, prevalence, and morphological features of the cystic stage of an apicomplexan parasite of native littleneck clams (*Protothaca staminea*) in British Columbia. *Journal of Parasitology*. 83:642-646.
 11. DUNHAM, J. S., B. KOKE, G. E. GILLESPIE, and G. MEYER. 2007. An exploratory survey for littleneck clams (*Protothaca staminea*) in the Broughton Archipelago, British Columbia - 2006. Canadian Manuscript Report of Fisheries and Aquatic Sciences. 2787:1-33.
 12. FEDER, H. M., J. C. HENDEE, P. HOLMES, G. J. MUELLER, and A. J. PAUL. 1979. Examination of reproductive cycle of *Protothaca staminea* using histology, wet weight/dry weight ratios, and condition indexes. *Veliger*. 22:182-187.
 13. FRASER, C. M., and G. M. SMITH. 1928. Notes on the ecology of the little neck clam, *Paphia staminea* Conrad. *Transactions of the Royal Society of Canada, Section V, Biological Sciences, Third Series Part 1*. XXII:249-269.
 14. FREESE, J. L., and C. E. OCLAIR. 1987. Reduced survival and condition of the bivalves *Protothaca staminea* and *Mytilus edulis* buried by decomposing bark. *Marine Environmental Research*. 23:49-64.
 15. FUKUYAMA, A. K., G. SHIGENAKA, and D. A. COATS. 2014. Status of intertidal infaunal communities following the Exxon Valdez oil spill in Prince William Sound, Alaska. *Marine Pollution Bulletin*. 84:56-69.
 16. FUKUYAMA, A. K., G. SHIGENAKA, and R. Z. HOFF. 2000. Effects of residual Exxon Valdez oil on intertidal *Protothaca staminea*: mortality, growth, and bioaccumulation of hydrocarbons in transplanted clams. *Marine Pollution Bulletin*. 40:1042-1050.
 17. GILLESPIE, G. E., and N. F. BOURNE. 2005. Exploratory intertidal bivalve surveys in British Columbia - 2004. Canadian Manuscript Report of Fisheries and Aquatic Sciences. 2734:1-144,VIII.
 18. GREY, M., P. G. LELIEVRE, and E. G. BOULDING. 2007. Selection for prey shell thickness by the naticid gastropod *Euspira lewisii* (Naticidae) on the bivalve *Protothaca staminea* (Veneridae). *Veliger*. 48:317-322.
 19. GROESBECK, A. S., K. ROWELL, D. L., and A. K. SALOMON. 2014. Ancient clam gardens increased shellfish production: adaptive strategies from the past can inform food security today. *Plos One*. 9.
 20. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 21. HANCOCK, D. R., T. F. GAUMER, G. B. WILLEKE, G. P. ROBART, and J. FLYNN. 1979. Subtidal clam populations: distribution, abundance, and ecology. Oregon State University, Sea Grant College Program, Corvallis.
 22. HILLMAN, R. E., and H. E. BENNETT. 1979. The fourth fold and secretory ridge of the mantle edge of the littleneck clam, *Protothaca staminea*. *Proceedings National Shellfisheries Association*. 69:195-195.
 23. HOUGHTON, J. P. 1977. Age and growth of *Protothaca staminea* and *Saxidomus giganteus* at Kiket Island Washington, USA. *Proceedings National Shellfisheries Association*. 67:119-119.
 24. JUANES, F., and E. B. HARTWICK. 1990. Prey size selection in Dungeness Crabs: the effect of claw damage. *Ecology*. 71:744-758.
 25. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.

26. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
27. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
28. LAZO, D. G. 2004. Bivalve taphonomy: testing the effect of life habits on the shell condition of the littleneck clam *Protothaca staminea* (Mollusca : Bivalvia). *Palaios*. 19:451-459.
29. NICKERSON, R. B. 1977. A study of the littleneck clam *Protothaca staminea* and the butter clam *Saxidomus giganteus* in a habitat permitting coexistence, Prince William Sound, Alaska USA. Proceedings National Shellfisheries Association. 67:85-102.
30. ORR, J. W., D. T. DRUMM, R. VAN SYOC, K. P. MASLENIKOV, T. W. PIETSCH, D. E. STEVENSON, and R. R. LAUTH. 2013. An annotated checklist of bottom-trawled macroinvertebrates of Alaska, with an evaluation of identifications in the Alaska Fisheries Science Center Bottom-Trawl Survey Database. NPRB Project 1016 Final Report. North Pacific Research Board, Alaska.
31. PARKER, M. S., P. A. JUMARS, and L. L. LECLAIR. 2003. Population genetics of two bivalve species (*Protothaca staminea* and *Macoma balthica*) in Puget Sound, Washington. *Journal of Shellfish Research*. 22:681-688.
32. PEARSON, W. H., D. L. WOODRUFF, P. C. SUGARMAN, and B. L. OLLA. 1981. Effects of oiled sediment on predation on the littleneck clam, *Protothaca staminea*, by the Dungeness Cra, *Cancer magister*. *Estuarine Coastal and Shelf Science*. 13:445-454.
33. PEITSO, E., E. HUI, B. HARTWICK, and N. BOURNE. 1994. Predation by the naticid gastropod *Polinices lewisii* (Gould) on littleneck clams, *Protothaca staminea* (Conrad) in British Columbia. *Canadian Journal of Zoology*. 72:319-325.
34. PETERSON, C. H. 1982. The importance of predation and intraspecific and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. *Ecological Monographs*. 52:437-475.
35. —. 1983. Interactions between two infaunal bivalves, *Chione undatella* (Sowerby) and *Protothaca staminea* (Conrad), and two potential enemies, *Crepidula onyx* and *Cancer anthonyi* (Rathbun). *Journal of Experimental Marine Biology and Ecology*. 68:145-158.
36. PETERSON, C. H., and S. V. ANDRE. 1980. An experimental analysis of interspecific competition among marine filter feeders in a soft-sediment environment. *Ecology*. 61:129-139.
37. PETERSON, C. H., and M. L. QUAMMEN. 1982. Siphon nipping: its importance to small fishes and its impact on growth of the bivalve *Protothaca staminea* (Conrad). *Journal of Experimental Marine Biology and Ecology*. 63:249-268.
38. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
39. —. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
40. ROESIJADI, G. 1980. Influence of copper on the clam *Protothaca staminea*: effects on gills and occurrence of copper-binding proteins. *Biological Bulletin*. 158:233-247.
41. ROESIJADI, G., J. W. ANDERSON, and J. W. BLAYLOCK. 1978. Uptake of hydrocarbons from marine sediments contaminated with Prudhoe Bay crude oil: influence of feeding type of test species and availability of polycyclic aromatic hydrocarbons.

- Journal of the Fisheries Research Board of Canada. 35:608-614.
42. SCHMIDT, R. R., and J. E. WARME. 1969. Population characteristics of *Protothaca staminea* (Conrad) from Magu Lagoon, California. *Veliger*. 12:193-199.
 43. SHAW, W. N. 1986. Species profiles, life histories and environmental requirements of coastal fishes and invertebrates: Pacific Southwest common littleneck clam *Protothaca staminea*. U.S. Fish and Wildlife Service Biological Report: I-VI, 1-11.
 44. SWARTZ, R. C., W. A. DEBEN, and F. A. COLE. 1979. Bioassay for the toxicity of sediment to marine macrobenthos. *Journal Water Pollution Control Federation*. 51:944-950.
 45. TAKESUE, R. K., and A. VAN GEEN. 2004. Mg/Ca, Sr/Ca, and stable isotopes in modern and Holocene *Protothaca staminea* shells from a northern California coastal upwelling region. *Geochimica et Cosmochimica Acta*. 68:3845-3861.
 46. THOMAS, R. E., M. LINDEBERG, P. M. HARRIS, and S. D. RICE. 2007. Induction of DNA strand breaks in the mussel (*Mytilus trossulus*) and clam (*Protothaca staminea*) following chronic field exposure to polycyclic aromatic hydrocarbons from the Exxon Valdez spill. *Marine Pollution Bulletin*. 54:726-732.

Updated 2016

Nutricola tantilla

Phylum: Mollusca
Class: Bivalvia; Heterodonta
Order: Veneroida
Family: Veneridae

Taxonomy: Originally described under the name *Venus (Trigona) tantillus* based on shell structure characters by Gould in 1853, this species was transferred to the genus *Transennella* in 1884 by Dall. The latter genus is routinely seen in manuscripts (e.g., see Kabat 1986; Lindberg 1990; Gallucci and Kawaratani 1975; Falese et al. 2011). However, according to Bernard (1982), the genus *Transennella* is limited to warm and tropical regions of east and western America and he designated the new genus, *Nutricola* (for diagrammatic comparison of the two genera, see Fig. 1–2 Bernard 1982; but see Lindberg 1990). Members of the genus *Transennella* are characterized by a hinge with three cardinal teeth, an elongated anterior lateral tooth on the left valve, an angular pallial sinus, and a grooved inner ventral shell margin (Gray 1982). Two varieties of *N. tantilla* were noticed in 1970 (Gray 1982). Together, these varieties were previously synonymized with the sympatric species, *N. confusa* (designated in 1982 by Gray). But upon investigation of morphological characters of internal anatomy and shell morphology, a neotype of *N. tantilla* was designated (Gray 1982). Common synonyms for *N. tantilla* include: *Venus tantillus*, *Transennella tantilla* and other known synonyms include *Venus rhyssomia* and *Psephis tantillus* (Gray 1982).

Description

Size: A relatively small clam, adults up to 5–6 mm in length (Kozloff 1993). The illustrated specimen (Figs. 1–2) is 3.5 mm in length, 3.0 mm tall, and 1.6 mm in diameter. The weight can be determined by clam length: $\log \text{ weight (mg)} = -0.85598 + 3.09033 \log \text{ length (mm)}$; the average dry weight of the largest individuals collected in False Bay, Washington was 30.2 mg (Pamatmat 1966).
Color: Cream in color, with posterior (end that bears the siphons) one third of shell a purple brown color that radiates from the beak (Fig. 1). Shell interior is creamy white, with same purple or brown coloration. There is

occasionally a radial strip anteriorly (Oldroyd 1924; Kozloff 1993) (Figs. 3–4).

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007). *Nutricola tantilla* is a small venerid species, that is unique among venerids by its **byssus**, and an umbo that is situated almost exactly between anterior and posterior ends such that the clam looks like an isosceles triangle from the side (see Fig. 352, Kozloff 1993) (Fig. 1).

Body:

Color:

Interior: The ligament is completely external; there is no resilifer or internal ligament (Fig. 2).

Exterior:

Byssus: Byssal threads are fine and clear (Fig. 1a) and used for attachment to substrate, which is rare in Veneridae (Narchi 1970, 1971). Byssal gland in middle of foot, and threads also join young in brood pouch.

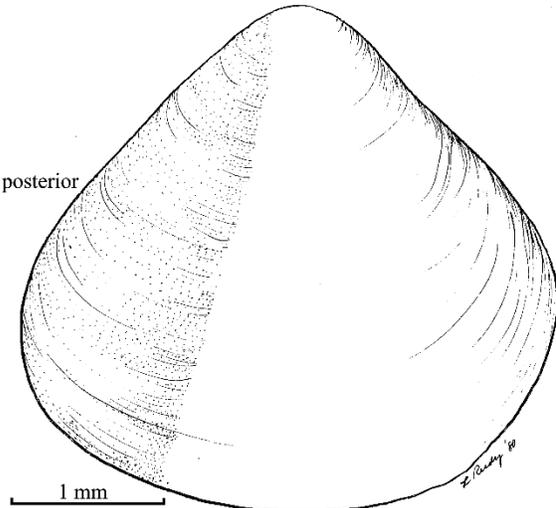
Gills:

Shell:

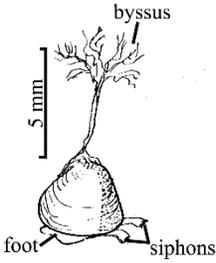
Interior: Ventral margin is smooth, i.e., not crenulated. The margin is with a few oblique grooves on inner ventral margin, but these are visible only with very high magnification. The pallial sinus is rounded, bent anteriorly, and parallel to the ventral margin; not bent sharply upward (Fig. 3).

Exterior: Overall shell shape is not unlike a rounded isosceles triangle (Kozloff 1993) (Fig. 1). Shape is elongate or oval, heavy, solid, slightly longer than high, and clearly triangular. Anterior and posterior dorsal margins are straight. The beaks are almost central, barely anterior to midline, often eroded (Kozloff 1974). The surface sculpture is with fine concentric grooves only, no other sculpture (Kozloff 1974). The valves are equal and not gaping. There is no rough periostracum, but byssal attachments (see **Byssus**) may cover part of surface.

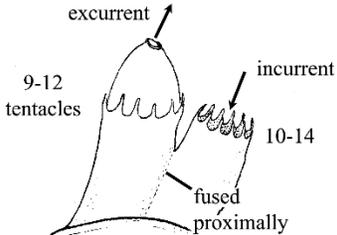
Nutricola tantilla



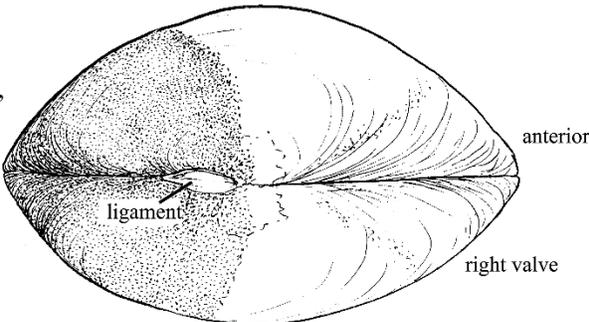
1. *Nutricola tantilla*, right valve (L:3.5mm, D:1.6mm, H:3.0mm) x28: shell solid, triangular; posterior third purple; fine concentric sculpture; no periostracum.



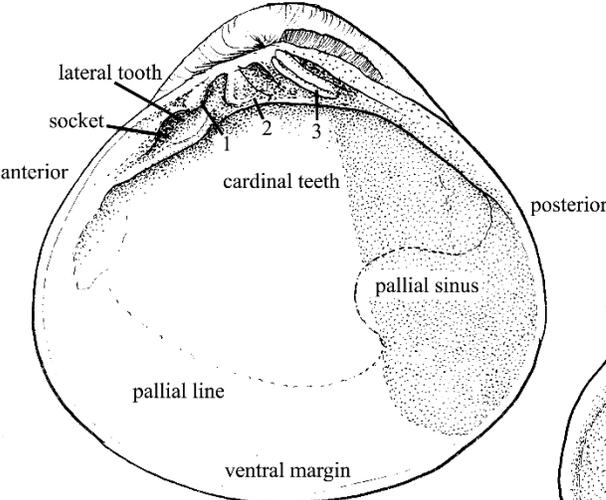
1a. Live clam x4



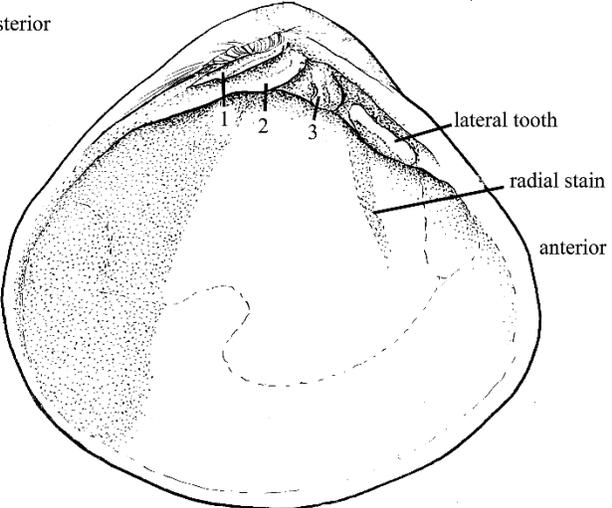
1b. Siphons



2. Exterior (dorsal view): valves equal; beaks almost central; ligament external; no gape to valves.



3. Interior, right valve: three divergent cardinal teeth, one anterior lateral tooth, socket; pallial sinus rounded; purple stain posteriorly; smooth ventral margin.



4. Interior, left valve: three cardinal teeth, one anterior lateral tooth; anterior radial purple stain.

Hinge: The hinge area has three divergent cardinal teeth in each valve (Figs. 3–4). The lateral teeth are conspicuous and there are anterior teeth in both valves. There is a socket for the lateral tooth in the right valve (Fig. 3).

Eyes:

Foot: The foot is large, and can bury individuals rather quickly.

Siphons: Siphons are short, sensitive, and extend only a few mm from body. The excurrent and incurrent siphons are fused proximally, with long tentacles that are flexible. There are 9–12 tentacles on the excurrent siphon and 10–14 on the incurrent (a defining character of this species, Maurer 1967b) (Fig. 1b).

Burrow: Individuals are hardly buried and found just under surface of sand (upper 1 cm layer) (Pamatmat 1969; Kozloff 1993); burial too deep leads to mortality in *N. tantilla* (Gallucci and Kawaratani 1975). The presence of byssal threads in this species may be explained by a need to maintain location despite a shallow burrow (Narchi 1970).

Possible Misidentifications

Veneroida is a large bivalve order, characterized by well-developed hinge teeth, including most heterodonts. The family Veneridae is characterized by a hinge without lateral teeth, ligament that is entirely external, radial ribs on shell exterior, and three cardinal teeth on each shell valve. There are 12–16 species reported locally in this family within the genera *Nutricola*, *Saxidomus*, and *Leukoma*, with two species in each, and *Gemma gemma*, *Irusella lamellifera*, *Tivela stultorum*, *Venerupis philippinarum*, *Mercenaria mercenaria*, *Callithaca tenerrima*, each with a single species represented locally.

Nutricola species are small, with shells usually less than 10 mm in length. This genus is defined by a small, ovate shell, inconspicuous beaks, a sunken ligament, and ventral shell margins with weak longitudinal ridges; the genus originated in the Miocene (Bernard 1982). *Gemma gemma* also has a small shell, but it is triangular in shape compared to *Nutricola* species with elongate or oval shells. *Tivela stultorum* also has a triangular shell, but individuals are larger than *G. gemma* and have a smooth shell surface

with shiny periostracum. *Gemma gemma*, the small (about 2.5 mm) purple-marked Atlantic bivalve, can be common in bay mud (for comparison of *N. tantilla* (as *V. tantillus*) and *G. gemma*, see Bernard 1982 and Narchi 1971). It is triangular, and no longer than high, its left hinge lacks the characteristic anterior lateral tooth of *N. tantilla* and **byssus**. Its ventral margin is finely crenulate, not smooth and its pallial sinus is bent sharply upward, not rounded and angled anteriorly. *Gemma* often has *Enteromorpha* attached to its posterior and it can be found in the same habitat as *N. tantilla* (e.g., Puget Sound, Washington) but in California (Tomales Bay, California) it occupies a different niche (Narchi 1971). *Nutricola tantilla* has a shell that is white in color and siphons that are fused (or nearly so) at the tips. *Nutricola confusa* has a shell that is purple in color, siphons that bear a conspicuous cleft as well as conspicuous anterior lateral teeth, which are weak in *N. tantilla*. *Gemma* species also have a series of tiny teeth along the inside lower margin of one valve, which are lacking in *N. tantilla* (Kozloff 1993).

Nutricola tantilla has purple markings, an eroded beak, and clearly marked concentric lines on its shell. Its hinge plate is wide, its anterior tooth well-developed, and it has split siphons (for half their length), with flexible tentacles (9–12 on the excurrent, 10–14 on the incurrent siphon, Fig. 1b)). *Nutricola confusa* is all white, without purple on the posterior, with only an occasional brown slot anterior to its beaks. The beaks are prominent, not eroded and the shell sculpture is faint, consisting of numerous fine lines. The hinge plate is narrow, and the anterior tooth is thin and lamellar. This species has siphons fused for almost their whole length, and short stiff siphon tentacles, with 10–14 tentacles on the excurrent siphon, 11–16 on the incurrent one (Maurer 1967b). *Nutricola confusa*, also occurs from Coos Bay, Oregon to central California, and is the same size, but lacks the distinctive purple color of the shell evident in *N. tantilla* (see **Color**) (Russel and Huelsenbeck 1989; Kozloff 1993). The two species are very similar, but differ in the shell shape, degree of siphon fusion and tentacle number (Falese et al. 2011). (For full comparative morphology of the two species, see Gray 1982.)

The remaining species have shells larger than 10 mm in length. Some species have shell sculpturing that is dominated by commarginal ribs with fine radial ridges and others have shells that have radial ridges with inconspicuous, or not predominating, commarginal ribs. Of those in the former category, *I. lamellifera* has widely spaced commarginal lamellae and a shell that is short compared to *M. mercenaria* and *C. tenerrima*. The two latter species have elongated shells, no anterior lateral teeth and valves that do not gape. *Saxidomus* species also have an elongate shell, when compared to *I. lamellifera*, but they possess anterior lateral teeth and valves that are separated by a narrow gape, posteriorly. *Saxidomus nuttalli* and *S. giganteus* can be differentiated as the former species has a elongate and thinner shell as well as a narrow escutcheon (not present in *S. giganteus*). The shell sculpturing in *S. giganteus* also appears smooth as the commarginal ribs are thin, low and tightly spaced, while the opposite is true for *S. nuttalli*.

The venerid species without predominately commarginal ribs include *V. philippinarum* and members of the genus *Leukoma*. *V. philippinarum*, the introduced Japanese cockle (see Fig. 1a *Leukoma staminea*, description in this guide), with strong radial ribs and a prominent ligament, elongate oval shell and, like *N. tantilla*, a purple stain in the interior. *Leukoma* species differ from *V. philippinarum* by having an inner ventral margin that is not smooth, a ligament that is not prominent and fused siphons. *Leukoma staminea* has shell sculpturing that is dominated by numerous radiating ribs, with faint commarginal ridges and the opposite is true for its congener (i.e., dominant radiating and commarginal ridges).

Ecological Information

Range: Type locality is Santa Barbara, California. Known range includes the northeast Pacific from Sitka, Alaska, to southern California (Oldroyd 1924).

Local Distribution: Local distribution includes sites in Coos Bay and the South Slough channel edge).

Habitat: Sand or sandy mud in protected bays. This specimen was collected from clean sand at the channel edge. They are often in other shells, where they attach by

byssal threads. The presence of **byssus** may limit the ability of this species to spread geographically. They are also found among eelgrass (e.g., *Zostera* spp., *Phyllospadix* spp.) roots (Obreski 1968), and in firm mud or sandy gravel (Smith 1960). They are nearly always in top centimeters of the sediment (Smith 1960). *Nutricola tantilla* can tolerate turbidity by remaining closed for long periods to avoid the deleterious effects of sediment burial (Maurer 1967b). The largest number of *N. tantilla* were observed in a combination of silt and clay habitats, with sediment size less than 63 μm , although individuals were also observed in fine (> 63 μm), medium (> 250 μm , and coarse (> 500 μm) sand (see Table 1 Tomales Bay, California, Maurer 1967b).

Salinity: Full seawater, collected at salinities of 30.

Temperature: Cold to temperate waters (e.g. 8–11°C, Pamatmat 1969), as indicated by geographical range.

Tidal Level: Low intertidal, top 2.5 cm of sand and mud (Kabat and O'Foighil 1987), as well as offshore down to 35 m (Keen and Coan 1974). Most dense at mean lower low water (False Bay, Washington, Pamatmat 1969).

Associates: Heavily infested by the trematodes, *Telolecithus pugetensis* and *Parvaterma* (Obreski 1968; Ruiz 1991). In *Telolecithus pugetensis*, *N. tantilla* is the first, and sometimes the second, intermediary host. *Nutricola tantilla* ingests trematode eggs, which, as sporocysts, destroy much of its visceral mass and gonads; infected adults are sterile (Tomales Bay, DeMartini and Pratt 1964). Gametes are reduced and sometimes completely removed by the presence of parasitic trematode larvae (Kabat 1985, 1986; Kabat and O'Foighil 1987). *Nutricola tantilla* occasionally, co-occurs with the congener *N. confusa* and the clam, *Macoma inquinata*. Parasitism by the digenetic trematode, *Parvaterma borealis*, leads to genetic resistance over time (Grosholz 1994).

Abundance: Individuals most dense at mean lower low water in troughs between sandbars. *Nutricola tantilla* can be one of the numerically dominant animals (Puget Sound, Washington. The local density was measured as 1,500–2,500/m² (South Slough, Coos Bay) (Asson, pers com.).

Life-History Information

Reproduction: Reported as a protandrous hermaphrodite by some (Hansen 1953; Gray 1982; Kabat and O'Foighil 1987) and dioecious by others (see Lutzen et al. 2015); viviparous. Individuals broods young within chamber: eggs and young of all stages can be found in the brood chamber between inner gill and body wall, i.e., the inner demibranch (see Fig. 2, Kabat 1985; Falese et al. 2011) (*Nutricola* = "little nurse", Bernard 1982). A single brood can contain individuals spanning a range of developmental stages (Kabat 1985; Russell and Huelsenbeck 1989; Falese et al. 2011). Sperm of *Nutricola* are modified, i.e., long and needle-shaped heads, the tail of *N. tantilla* is longer and wider than those of the congener, *N. confusa* (see Fig. 2, Geraghty et al. 2008; Falese et al. 2011), they are packaged into a spermatozeugmata (see Fig. 1 Falese et al. 2011). Males elicit what is called "spermcasting" in which they broadcast spawn sperm while females retain eggs, which are later fertilized within the female brood chamber (Geraghty et al. 2008; Falese et al. 2011). The sperm most likely enters the female chamber via the siphon (Geraghty et al. 2008) and females likely store sperm within nonepithelial tissue until use (Lutzen et al. 2015). The head piece that is 17–18 μm in length and flagellum 48 μm long (for sperm cell ultrastructure, see Lutzen et al. 2015); oocytes are approximately 250 μm in diameter (Hansen 1953; Kabat and O'Foighil 1987). Gametes are released into space between the inner gill and visceral mass where they are brooded until they are released as juveniles (Kabat and O'Foighil 1987; Brink 2001). Brood size estimates vary from with up to 40 (Kozloff 1993) to 300 (Kabat and O'Foighil 1987) embryos per brood, in a mass surrounded by an envelope, and is dependent on the size of the individual brooding (number of embryos increases in proportion to the adult length cubed, Kabat 1985). Nearly all large clams, which are mostly female, will have broods throughout the year. There is no clear spawning period, but young are released only during summer months (Hansen 1953; Kozloff 1993; Kabat and O'Foighil 1987). *Nutricola tantilla* are among the smallest clams, and males and females are found in equal numbers (Hansen 1953). Their fecundity is affected by, what are sometimes sterilizing, trematode

sporocysts (see **Associates**, DeMartini and Pratt 1964). Broods observed in early spring (May–June) in False Bay, Washington (Gray 1982).

Larva: Development takes place in mantle cavity (see **Reproduction**) and the size of adult determines number of the young. Larvae are without a velum, or pelagic stage (Hansen 1953). The oldest larval stage was approximately 650 μm in length (Hansen 1953). Some bivalve species (e.g. *Mytilus edulis*, *Macoma balthica*) have two dispersal periods. The initial larval dispersal and settlement into the benthos, is followed by potential dispersal from the benthos by thread drifting on water currents via mucous threads by juveniles (i.e., "thread drifting", Martel and Chia 1991).

Juvenile: Males reach sexual maturity at 3.5–4mm in length, while females mature at larger sizes, 3.5–7 mm in length (Kabat and O'Foighil 1987). The smallest adults with eggs were 3.2 mm in length (Pamatmat 1966).

Longevity: *Nutricola tantilla* longevity is probably a little over one year (Hansen 1953; Kabat and O'Foighil 1987).

Growth Rate: In four months, individuals grow 4 mm and from 2.6 mg to 30 mg (September); the total weight gain per individual is 0.953 mg per month (Hansen 1953; Pamatmat 1966). In 2000, Jacobs et al. found, through in-situ hybridization, that gene expression involved in early development of cells surrounding the shell valves appears to have a single evolutionary origin for skeletogenesis in all bilaterian phyla (see Jacobs et al. 2000).

Food: *Nutricola tantilla* is a suspension feeder that eats small particles (not a deposit feeder) (Norchi 1971). Feeding may primarily occur at night (Obreski 1968). Common foods include diatoms in the following genera: *Navicula*, *Coscinodiscus*, as well as *Nitzschia* and *Melosira* (Maurer 1967b).

Predators: Known predators include fish (e.g., *Cymatogaster* (surf perch)) and trematodes (see also **Associates**) (DeMartini and Pratt 1964), shorebirds, and some gastropods (Obreski 1968). The nonindigenous green crab, *Carcinus maenas*, also preys upon and reduces the population density of both *N. tantilla* and *N. confusa* (Grosholz et al. 2000).

Behavior: Individuals can bury themselves in less than a minute if disturbed (Norchi 1971), but they can be found on or near the surface when feeding.

Bibliography

1. BERNARD, F. R. 1982. *Nutricola* new genus for *Transennella tantilla* from the northeastern Pacific Bivalvia Veneridae. *Venus: The Japanese Journal of Malacology*. 41:146-149.
2. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.). Oregon State University Press, Corvallis, OR.
3. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
4. DEMARTINI, J., and I. PRATT. 1964. The life cycle of *Telolecithus pugentensis* Lloyd and Guberiet, 1932. *Journal of Parasitology*. 50:101-105.
5. FALESE, L. E., M. P. RUSSELL, and N. R. DOLLAHON. 2011. Spermcasting of spermatozeugmata by the bivalves *Nutricola confusa* and *N. tantilla*. *Invertebrate Biology*. 130:334-343.
6. GALLUCCI, V. F., and R. K. KAWARATANI. 1975. Mortality of *Transennella tantilla* due to burial. *Journal of the Fisheries Research Board of Canada*. 32:1637-1640.
7. GERAGHTY, J., M. P. RUSSELL, and N. DOLLAHON. 2008. A Quantitative assessment of spermatozoan morphology in *Nutricola confusa* and *Nutricola tantilla* (Bivalvia: Veneridae). *Veliger*. 50:263-268.
8. GRAY, S. 1982. Morphology and taxonomy of two species of the genus *Transennella* (bivalvia:veneridae) from western North America and a description of *T. confusa* sp. nov. *Malacological Review*. 15:107-117.
9. GROSHOLZ, E. D. 1994. The effects of host genotype and spatial distribution on trematode parasitism in a bivalve population. *Evolution*. 48:1514-1524.
10. GROSHOLZ, E. D., G. M. RUIZ, C. A. DEAN, K. A. SHIRLEY, J. L. MARON, and P. G. CONNORS. 2000. The impacts of a nonindigenous marine predator in a California bay. *Ecology*. 81:1206-1224.
11. HANSEN, B. 1953. Brood protection and sex ratio of *Transennella tantilla* (Gould), a Pacific bivalve. *Videnskabelige Meddelelser Dansk Naturhistorisk Forening*. 115:313-324.
12. JACOBS, D. K., C. G. WRAY, C. J. WEDEEN, R. KOSTRIKEN, R. DESALLE, J. L. STATON, R. D. GATES, and D. R. LINDBERG. 2000. Molluscan engrailed expression, serial organization, and shell evolution. *Evolution & Development*. 2:340-347.
13. KABAT, A. R. 1985. The allometry of brooding in *Transennella tantilla* (Gould (Mollusca, Bivalvia)). *Journal of Experimental Marine Biology and Ecology*. 91:271-279.
14. —. 1986. Effects of trematode parasitism on reproductive output of the bivalve *Transennella tantilla*. *Canadian Journal of Zoology*. 64:267-270.
15. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
16. KOZLOFF, E. N. 1974. Keys to the marine invertebrates of Puget Sound, the San Juan Archipelago, and adjacent regions. University of Washington Press, Seattle.
17. —. 1983. Seashore life of the northern Pacific coast. University of Washington Press, Seattle.
18. LINDBERG, D. R. 1990. *Transennella dall* versus *Nutricola bernard* (Bivalvia, Veneridae): an argument for evolutionary systematics. *Journal of Molluscan Studies*. 56:129-132.
19. LUETZEN, J., A. JESPERSEN, and M. P. RUSSELL. 2015. The Pacific clam *Nutricola tantilla* (Bivalvia: Veneridae) has separate sexes and

- makes use of brood protection and sperm storage. *Journal of Molluscan Studies*. 81:397-406.
20. MARTEL, A., and F. S. CHIA. 1991. Drifting and dispersal of small bivalves and gastropods with direct development. *Journal of Experimental Marine Biology and Ecology*. 150:131-147.
 21. MAURER, D. 1967. Filtering experiments on marine pelecypods from Tomales Bay, California. *The Veliger*. 9:305-309.
 22. —. 1969. Pelecypod sediment association in Tomales Bay California. *Veliger*. 11:243-249.
 23. NARCHI, W. 1970. The presence of byssus in adults of *Transennella tantilla* (Gould) (Bivalvia: Veneridae). *Wasmann Journal of Biology*. 28:233-236.
 24. —. 1971. Structure and adaptation in *Transennella tantilla* (Gould) and *Gemma gemma* (Totten) (Bivalvia, Veneridae). *Bulletin of Marine Science*. 21:866-885.
 25. OBRESKI, S. 1968. On the population ecology of two intertidal invertebrates and the paleoecological significance of size-frequency distributions of living and dead shells of the bivalve *Transennella tantilla*. Ph.D. University of Chicago, Chicago.
 26. OLDROYD, I. S. 1924. Marine shells of Puget Sound and vicinity. University of Washington Press, Seattle.
 27. PAMATMAT, M. M. 1966. The ecology and metabolism of a benthic community on an intertidal sandflat (False Bay, San Juan Island, Washington). Ph.D. University of Washington, Seattle.
 28. —. 1969. Seasonal Respiration of *Transennella tantilla* (Gould). *American Zoologist*. 9:418-26.
 29. RUIZ, G. M. 1991. Consequences of parasitism to marine invertebrates: host evolution. *American Zoologist*. 31:831-839.
 30. RUSSELL, M. P., and J. P. HUELSENBECK. 1989. Seasonal variation in brood structure of *Transennella confusa* (Bivalvia, Veneridae). *Veliger*. 32:288-295.
 31. SMITH, L. S. 1960. Observations of *Transennella tantilla*, and ovoviviparous clam of the family Veneridae. Friday Harbor Laboratory.

Updated 2016

Saxidomus giganteus

Phylum: Mollusca
Class: Bivalvia; Heterodonta
Order: Veneroida
Family: Veneridae

Beefsteak clam, butter, or Washington clam

Taxonomy: Originally described as *Venerupis gigantea*, other synonyms include conflicts of taxonomic genus-species gender agreement, as *Saxidomus* is feminine (article 31.2, ICZN): *S. gigantea* (e.g., Paul et al. 1976; Robinson and Breese, 1982; Bendell 2014), as well as *Venus maxima*.

Description

Size: Adults average 10 cm in length (Paul et al. 1976; Kozloff 1993).

Color: Shell exterior is whitish, but can also have patches of blackish discoloration; juvenile exterior is sometimes tan in color (Kozloff 1993). The shell interior is also white.

General Morphology: Bivalve mollusks are bilaterally symmetrical with two lateral valves or **shells** that are hinged dorsally and surround a mantle, head, **foot** and viscera (see Plate 393B, Coan and Valentich-Scott 2007).). The Veneroida is a large and diverse bivalve heterodont order that is characterized by well-developed hinge teeth. There are 22 local families, and members of the Veneridae have three cardinal teeth on each valve (see Fig 302, Kozloff 1993; Plate 396H, Coan and Valentich-Scott 2007) (Fig. 4).

Body:

Color:

Interior: The ligament is completely external, and is seated on a long, massive nymph, or chondrophore (Fig. 4). The body tissue is rubbery and is “superb for chowder” (Kozloff 1993). Maximal systolic pressure was recorded for *Tresus capax* (see description in this guide) to be 13 cm H₂O, which is higher than 11 cm H₂O recorded for *Saxidomus giganteus* (Florey and Cahill 1977).

Exterior:

Byssus:

Gills:

Shell: The shell is oval in shape (Coan and Carlton 1975), and the posterior is truncate (Keen and Coan 1974).

Interior: The valves are similar in shape. The inner ventral margin is smooth

(Keen and Coan 1974), and the inner surface is white and porcelaneous. The muscle scars are dark and subequal in size. The pallial line is continuous (but broken by a sinus), not a series of scars (Fig. 3). The flesh is often reddish, hence one common name, the beefsteak clam.

Exterior: Exterior sculpture is with raised concentric growth lines and grooves, with no radial lines (Fig. 1). The valves are very similar, the shell is thick, heavy, and deep (Fig. 2). The most prominent lines representing periods of slowed growth (Kozloff 1993). The valves gape only slightly at posterior end (gape less than 1/4 shell width) (Kozloff 1993). Individuals can retract their siphon, but not feet. The shell microstructure was described for many veneroid clams by Shimamoto (1986), where *Saxidomus* species were characterized by a Type I shell composed of both composite prismatic and crossed lamellar structure (Shimamoto 1986).

Hinge: The hinge is very thick, heavy, and is posterior and external. There are three cardinal hinge teeth, flanked by a long lateral tooth in each valve (Fig. 4).

Eyes:

Foot:

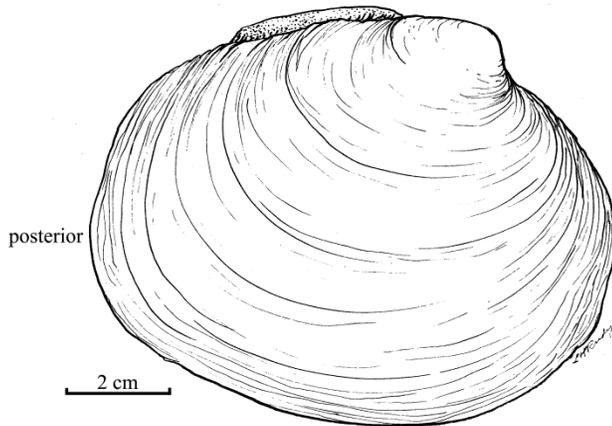
Siphons:

Burrow: Inhabits burrows up to 30 cm deep (Kozloff 1993). The burrow opening is recognizable by a cigar-shaped or deflated figure eight-shaped hole that is 1.2–2 cm long (Jacobson 1975).

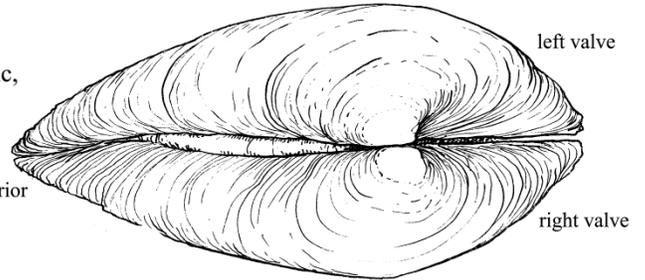
Possible Misidentifications

Veneroida is a large bivalve order, characterized by well-developed hinge teeth, including most heterodonts. The family Veneridae is characterized by a hinge without lateral teeth, ligament that is entirely external, radial ribs on shell exterior, and three cardinal teeth on each shell valve. There are 12–16 species reported locally in this family within the genera *Nutricula*, *Saxidomus*, and *Leukoma*, with two species in each, and *Gemma gemma*, *Irusella lamellifera*, *Tivela*

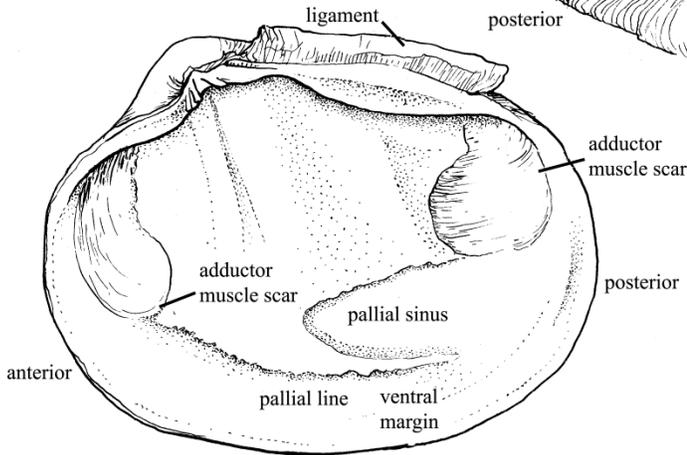
Saxidomus giganteus



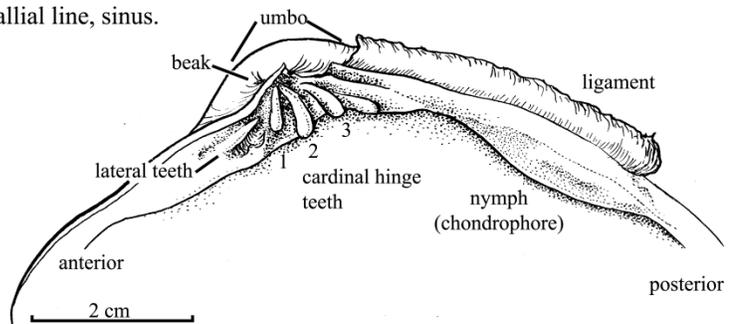
1. *Saxidomus giganteus*, exterior, right valve x1:
shell whitish, oval; posterior truncate; concentric,
rough ribs close together; valves similar,
thick, heavy.



2. Exterior (dorsal view):
valves similar, deep; hinge
heavy, ligament external.



3. Interior, right valve:
margin smooth, surface white, porcelaneous;
muscle scars similar; strong pallial line, sinus.



4. Interior, right valve (dorsal region) x1.5:
three cardinal hinge teeth; ligament seated
on nymph; long lateral teeth.

stultorum, *Venerupis philippinarum*, *Mercenaria mercenaria*, *Callithaca tenerrima*, each with a single species represented locally.

Nutricola species are small, with shells usually less than 10 mm in length. *Gemma gemma* also has a small shell, but it is triangular in shape compared to *Nutricola* species with elongate or oval shells. *Tivela stultorum* also has a triangular shell, but individuals are larger than *G. gemma* and have a smooth shell surface with shiny periostracum.

The remaining species have shells larger than 10 mm in length. Some species have shell sculpturing that is dominated by commarginal ribs with fine radial ridges and others have shells that have radial ridges with inconspicuous, or not predominating, commarginal ribs. Of those in the former category, *I. lamellifera* has widely spaced commarginal lamellae and a shell that is short compared to *M. mercenaria* and *C. tenerrima*. The two latter species have elongated shells, no anterior lateral teeth and valves that do not gape. *Saxidomus* species also have an elongate shell, when compared to *I. lamellifera*, but they possess anterior lateral teeth and valves that are separated by a narrow gape, posteriorly. *Saxidomus nuttalli* and *S. giganteus* can be differentiated as the former species has an elongate and thinner shell as well as a narrow escutcheon (not present in *S. giganteus*). The shell sculpturing in *S. giganteus* also appears smooth as the commarginal ribs are thin, low and tightly spaced, while the opposite is true for *S. nuttalli*. Its shell is more elongate, the ribs heavier, rougher and more conspicuous (Coan and Carlton 1975) and the interior is often marked posteriorly with purple. *Saxidomus nuttalli*, the larger, more southern species, is found in California in the same habitat as *S. giganteus*, but apparently does not extend into Oregon. (*S. nuttalli* is the only *Saxidomus* in Humboldt Bay, however). *Saxidomus nuttalli*, referred to as the “money clam” because of its representation as currency for Californian native American tribes (Ricketts and Calvin 1952), resembles *S. giganteus*, but is larger (ironically, 12.7 compared to 7.6 cm) and has more prominent growth lines and a shell that is purplish at the siphonal end ((Ricketts and Calvin 1952; Kozloff 1993). *Saxidomus nuttalli* is more

common in the southern end of its distribution, while *S. giganteus* is more common north (Ricketts and Calvin 1952).

Panopea generosa, the deep-burrowing geoduck, is quadrate, and gapes widely. *Tresus capax*, the gaper clam, (family Mactridae, see description in this guide), is also quadrate, fairly smooth with chalky white shell exterior. The truncated posterior gapes moderately, its ligament is partly internal, the cardinal teeth are "A" shaped, and the shell has a dark, eroded partial covering.

Ecological Information

Range: Type locality is not specified (see Orr et al. 2013). Known range includes the Aleutian Islands, Alaska to Monterey, California; *S. giganteus* is rare in the southern range.

Local Distribution: Locally occurs in bays and estuaries, rarely on open coast or inlets with oceanic influence (Packard 1918). Common from Alaska to San Francisco Bay, California, but rare south of Humboldt bay, California (Kozloff 1993).

Habitat: Occurs in mud or sand (Coan and Carlton 1975), gravelly beaches (Puget Sound, Washington). “Clam gardens”, created adjacent to intertidal rock walls constructed by human populations in the Holocene, have four times as many *S. giganteus* and twice as many *P. staminea* (see description in this guide) individuals as non-walled beaches, and transplanted juveniles of the latter species also grow faster (1.7 times faster) in clam gardens (Groesbeck et al. 2014).

Salinity: Occurs in sites with average yearly salinity is 29 (range 24–32, Puget Sound, Washington Goong and Chew 2001).

Temperature: Individuals prefer temperate-cold waters (see **Range**).

Tidal Level: Individuals most commonly collected from just under the sediment surface, but also found up to 30 cm deep.

Associates: Occasionally infested with immature specimens of commensal pea crab *Pinnixa littoralis*, but usually free of symbiotic or parasitic associates (Ricketts and Calvin 1971). Co-occurs with other clams, *Tapes philippinarum* and *Protothaca staminea* as well as the shore crab, *Hemigrapsus* (Nickerson 1977; Goong and Chew 2001). *Protothaca staminea* and *S. giganteus* co-occur on Kiket Island, Washington, where the

greatest diversity and richness of other marine invertebrates are found (Houghton 1977). Co-occurs with other clams (e.g., *Tresus capax* and *T. nuttallii*, Gillispie and Bourne 2004; *Sanguinolaria nuttallii*, Peterson and Andre 1980), and the presence of the latter species is negatively effected by *S. nuttallii* (Peterson and Andre 1980).

Abundance: "The most abundant clam of the Northwest" (Ricketts and Calvin 1971), *Saxidomus giganteus* was a commercially harvested species in Puget Sound, Washington (Kozloff 1974). Up to 352 individuals/m² were reported from beaches in British Columbia, Canada (Gillespie and Bourne 2005). In British Columbia beaches, assessed in 1993, *S. giganteus* density was as high as 376 individuals/m² (Gillispie and Bourne 2004).

Life-History Information

Reproduction: Separate sexes reproduce by free-spawning, external fertilization and development via a free-swimming larva. Oocytes are 80–90 µm in diameter and surrounded by a jelly layer that is 230 µm in diameter (see Fig. 1, Breese and Phibbs 1970). Spawning from March–June has been reported for the Oregon coast (Fraser 1929; Robinson and Breese 1982; Kabat and O'Foighil 1987). Gametogenesis occurs in fall months and is complete by August and September in the Strait of Georgia (Fraser 1929). Like *Protothaca staminea*, spawning in response to dense algal blooms has been reported (Robinson and Breese 1982). There is considerable variation in spawning times, even in neighboring beds with variable water temperatures. Polar body formation occurs 60 minutes post fertilization and cleavage begins 30 minutes later; trochophore larvae develop after 24 hours, which become bivalve veliger larvae 24 hours later (18°C, see Fig. 1, Breese and Phibbs 1970).

Larva: Bivalve development generally proceeds from external fertilization via broadcast spawning through a ciliated trochophore stage to a veliger larva. Bivalve veligers are characterized by a ciliated velum that is used for swimming, feeding and respiration. The veliger larva is also found in many gastropod larvae, but the larvae in the two groups can be recognized by shell morphology (i.e. snail-like versus clam-like). In bivalves, the initial shelled-larva is called a

D-stage or straight-hinge veliger due to the "D" shaped shell. This initial shell is called a prodissoconch I and is followed by a prodissoconch II, or shell that is subsequently added to the initial shell zone (see Fig. 1, Caddy 1969). Finally, shell secreted following metamorphosis is simply referred to as the dissoconch (see Fig. 2, Brink 2001). Once the larva develops a foot, usually just before metamorphosis and loss of the velum, it is called a pediveliger (see Fig. 1, Caddy 1969; Kabat and O'Foighil 1987; Brink 2001). (For generalized life cycle see Fig. 1, Brink 2001). Veliger larvae of *S. giganteus* are free-swimming for up to 30 days and grow approximately 7 µm per day (Breese and Phibbs 1970). They are straight hinge (see Fig. 4, Brink 2001) until they are 160 µm in length after 2 weeks (Fraser and Smith 1928). They have an anterior end that is longer and more pointed than the posterior, which is broadly rounded (Brink 2001). Throughout development, the umbo and both ends (ant and post) become broadly rounded and larvae are longer than they are tall. Larvae metamorphose at about 230 µm and (Brink 2001) have a pelagic duration of 4 wks (Fraser and Smith 1928; Kabat and O'Foighil 1987). Optimal growth and survival for larvae were obtained at 15°C, salinity 20–29, when fed a mixture of three algal species (settlement at 20–25 days when larvae were 230–250 µm, Bourne 1971).

Juvenile: Juvenile growth was 18 µm per day for 150 days post metamorphosis (Breese and Phibbs 1970, see also Walne 1973).

Longevity: To 20 years or more (Paul et al. 1976; Haderlie 1980).

Growth Rate: There is little growth of young individuals immediately after settling. Instead juveniles grow considerably the following spring (Fraser and Smith 1928). Growth rates varied for clams collected in different sites around Puget Sound, Washington, with oldest clams (e.g., 30 years) being 95–140 mm in length (Goong and Chew 2001, see also Gillespie and Bourne 2005). Growth rates are measured by annular rings, which are formed during periods of slowed growth, usually in winter months (Paul et al. 1976). Periods of growth may be slowed by reduction in salinity (Gillikin et al. 2005) and growth may be density dependent (Kline 1982). Specimens reached 65 mm in length after 8–9 years on

Porpoise Island, southeast Alaska (Paul et al. 1976). At three beaches in British Columbia where populations were measured in 1993, individuals 40–71 mm in length were 8 years old, 24–93 mm were 2–16 years, and 25–67 mm were 2–12 years old; estimating that individuals 6.5 years old are approximately 63 mm in length (Gillispie and Bourne 2004). Legal catch size is 63 mm in length, which occurs when individuals are approximately 6–10 years old (Gillispie and Bourne 2004).

Food: A filter-feeder, that feeds by straining material from currents of water that are pumped through the gills. The ingestion and concentration of toxic algae (e.g., from the genera *Alexandrium*, *Gymnodinium*, *Pyrodinium*, Smolowitz and Doucette 1995) leads to paralytic shellfish poisoning, rendering the clams dangerous for human consumption (Kitts et al. 1992; Kitts and Smith 1992). Clams accumulate toxins in their siphon tips, in part, to reduce predation (Price and Lee 1972; Smolowitz and Doucette 1995). This suite of neurotoxins (50 structural variants) are collectively known as saxitoxins as they were first isolated from *S. giganteus* (Oshima et al. 1977; Vale 2010) and the chemical composition of this toxin was described by Schantz et al. (1974).

Predators: Known predators include sting rays, fishes, shore birds (e.g., gulls, Maron 1982), drilling snails, and sea otters (Kvitek and Oliver 1992; Kvitek et al. 1993, but see reduction in sea otter predation due to presence of saxitoxin, Kvitek et al. 1991). Predation by crab species, which break open the shells of many bivalves, is reduced by a larger and thicker shell, an inflated shell shape with steep ventral margin, and the ability to burrow deeply. Other bivalves (e.g., *Protothaca staminea*, see description in this guide) also close tightly, further reducing predation, however, the narrow posterior gape in *S. giganteus* allows for potential breaking by crab claws (Boulding 1984). *Octopus dofleini* are known to prey upon *S. giganteus* by drilling holes in their shells; increased shell thickness may reduce predation as incomplete boreholes were observed on thicker shelled clams (Ambrose et al. 1988). *Saxidomus giganteus* was historically (e.g., Burchell et al. 2013) and is currently a commercially important and harvested species; the most important food clam in British Columbia, Canada (Bourne

1971; Haderlie 1980; Kozloff 1993, see also Fig. 1 Gillispie and Bourne 2005). The fishery in southeast Alaska began in 1930 with a harvest of 11,340 kg (Paul et al. 1976) and in the Broughton Archipelago, British Columbia, Canada harvests as high as 500,000 kg were reported in 1970 (Dunham et al. 2006). (see Bechtol and Gustafson 1998 for commercial summary).

Behavior:

Bibliography

1. AMBROSE, R. F., B. J. LEIGHTON, and E. B. HARTWICK. 1988. Characterization of boreholes by *Octopus dofleini* in the bivalve *Saxidomus giganteus*. *Journal of Zoology*. 214:491-503.
2. BECHTOL, W. R., and R. L. GUSTAFSON. 1998. Abundance, recruitment, and mortality of Pacific littleneck clams *Protothaca staminea* at Chugachik Island, Alaska. *Journal of Shellfish Research*. 17:1003-1008.
3. BENDELL, L. I. 2014. Evidence for declines in the native *Leukoma staminea* as a result of the intentional introduction of the non-native *Venerupis philippinarum* in coastal British Columbia, Canada. *Estuaries and Coasts*. 37:369-380.
4. BOULDING, E. G., and T. K. HAY. 1984. Crab response to prey density can result in density-dependent mortality of clams. *Canadian Journal of Fisheries and Aquatic Sciences*. 41:521-525.
5. BOURNE, N. 1971. The effects of temperature, salinity and food on the development of the larvae of butter clams, *Saxidomus giganteus*. *Proceedings National Shellfisheries Association*. 61:1971-1971.
6. BREESE, W. P., and F. D. PHIBBS. 1969. Some observations on the spawning and early development of the butter clam, *Saxidomus giganteus*. *Proceedings National Shellfisheries Association*. 60:95-98.
7. BRINK, L. A. 2001. Mollusca: Bivalvia, p. 129-149. *In: Identification guide to larval marine invertebrates of the Pacific Northwest*. A. Shanks (ed.).

- Oregon State University Press,
Corvallis, OR.
8. BURCHELL, M., A. CANNON, N. HALLMANN, H. P. SCHWARCZ, and B. R. SCHOENE. 2013. Intersite variability in the season of shellfish collection on the central coast of British Columbia. *Journal of Archaeological Science*. 40:626-636.
 9. COAN, E. V., and P. VALENTICH-SCOTT. 2007. Bivalvia, p. 807-859. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 10. DUNHAM, J. S., B. KOKE, G. E. GILLESPIE, and G. MEYER. 2007. An exploratory survey for littleneck clams (*Protothaca staminea*) in the Broughton Archipelago, British Columbia - 2006. Canadian Manuscript Report of Fisheries and Aquatic Sciences. 2787:1-33.
 11. FLOREY, E., and M. A. CAHILL. 1977. Hemodynamics in Lamellibranch mollusks: confirmation of constant-volume mechanism of auricular and ventricular filling. Remarks on heart as site of ultrafiltration. *Comparative Biochemistry and Physiology. A-Physiology*. 57:47-52.
 12. FRASER, C. M. 1929. The spawning and free swimming larval periods of *Saxidomus* and *Paphia*. *Transactions of the Royal Society of Canada*. 23:195-198.
 13. FRASER, C. M., and G. M. SMITH. 1928. Notes on the ecology of the butter clam, *Saxidomus giganteus*. *Transactions of the Royal Society of Canada*. 22:271-286.
 14. GILLESPIE, G. E., and N. F. BOURNE. 2005. Exploratory intertidal bivalve surveys in British Columbia - 2004. Canadian Manuscript Report of Fisheries and Aquatic Sciences. 2734:1-144, VIII.
 15. GILLIKIN, D. P., F. DE RIDDER, H. ULENS, M. ELSKENS, E. KEPPENS, W. BAEYENS, and F. DEHAIRS. 2005. Assessing the reproducibility and reliability of estuarine bivalve shells (*Saxidomus giganteus*) for sea surface temperature reconstruction: implications for paleoclimate studies. *Palaeogeography Palaeoclimatology Palaeoecology*. 228:70-85.
 16. GOONG, S. A., and K. K. CHEW. 2001. Growth of butter clams, *Saxidomus giganteus* Deshayes, on selected beaches in the state of Washington. *Journal of Shellfish Research*. 20:143-147.
 17. GROESBECK, A. S., K. ROWELL, D. L., and A. K. SALOMON. 2014. Ancient clam gardens increased shellfish production: adaptive strategies from the past can inform food security today. *Plos One*. 9.
 18. HADERLIE, E. C., and D. P. ABBOTT. 1980. Bivalvia: the clams and allies, p. 355-410. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, California.
 19. HOUGHTON, J. P. 1977. Age and growth of *Protothaca staminea* and *Saxidomus giganteus* at Kiket Island Washington, USA. *Proceedings National Shellfisheries Association*. 67:119-119.
 20. INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 2016. Article 31.2.
 21. JACOBSON, R. W., P. HEIKKILA, and K. S. HILDERBRAND. 1975. Oregon's captivating clams. Oregon State University Extension Service, Sea Grant Marine Advisory Program, and Oregon Dept. of Fish and Wildlife, Corvallis, Or.
 22. KABAT, A. R., and D. O'FOIGHIL. 1987. Phylum Mollusca, Class Bivalvia, p. 309-353. *In: Reproduction and development of marine invertebrates of the northern Pacific Coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 23. KEEN, A. M., and E. COAN. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, CA.
 24. KITTS, D. D., and D. S. SMITH. 1992. Cross-reacting antigens in the butter clam (*Saxidomus giganteus*) and their relationship to total paralytic shellfish poison toxicity. *Toxicon*. 30:967-976.

25. KITTS, D. D., D. S. SMITH, M. K. BEITLER, and J. LISTON. 1992. Presence of paralytic shellfish poisoning toxins and soluble proteins in toxic butter clams (*Saxidomus giganteus*). *Biochemical and Biophysical Research Communications*. 184:511-517.
26. KLINE, T. C. 1984. The effect of population density on the growth of the butter clam, *Saxidomus giganteus*. *Journal of Shellfish Research*. 3:112-112.
27. KOZLOFF, E. N. 1974. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago and adjacent regions. University of Washington Press, Seattle and London.
28. —. 1993. Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia. University of Washington Press, Seattle.
29. KVITEK, R. G., C. E. BOWLBY, and M. STAEDLER. 1993. Diet and foraging behavior of sea otters in southeast Alaska. *Marine Mammal Science*. 9:168-181.
30. KVITEK, R. G., A. R. DEGANGE, and M. K. BEITLER. 1991. Paralytic shellfish poisoning toxins mediate feeding behavior in sea otters. *Limnology and Oceanography*. 36:393-404.
31. KVITEK, R. G., and J. S. OLIVER. 1992. Influence of sea otters on soft-bottom prey communities in southeast Alaska. *Marine Ecology Progress Series*. 82:103-113.
32. MARON, J. L. 1982. Shell-dropping behavior of western gulls (*Larus occidentalis*). *Auk*. 99:565-569.
33. NICKERSON, R. B. 1977. A study of the littleneck clam *Protothaca staminea* and the butter clam *Saxidomus giganteus* in a habitat permitting coexistence, Prince William Sound, Alaska USA. *Proceedings National Shellfisheries Association*. 67:85-102.
34. ORR, J. W., D. T. DRUMM, R. VAN SYOC, K. P. MASLENIKOV, T. W. PIETSCH, D. E. STEVENSON, and R. LAUTH. 2013. An annotated checklist of bottom-trawled macroinvertebrates of Alaska, with an evaluation of identifications in the Alaska Fisheries Science Center Bottom-Trawl Survey Database. NPRB Project 1016 Final Report. North Pacific Research Board, Alaska.
35. OSHIMA, Y., L. J. BUCKLEY, M. ALAM, and Y. SHIMIZU. 1977. Heterogeneity of paralytic shellfish poisoning: three new toxins from cultured *Gonyaulax tamarensis* cells, *Mya arenaria* and *Saxidomus giganteus*. *Comparative Biochemistry and Physiology: C-Pharmacology Toxicology & Endocrinology*. 57:31-34.
36. PACKARD, E. L. 1918. Molluscan fauna from San Francisco Bay. *Zoology*. 14:199-452.
37. PAUL, A. J., J. M. PAUL, and H. M. FEDER. 1976. Age, growth and recruitment of the butter clam, *Saxidomus gigantea* on Porpoise Island, Southeast Alaska, USA. *Proceedings National Shellfisheries Association*. 66:26-28.
38. PETERSON, C. H., and S. V. ANDRE. 1980. An experimental analysis of interspecific competition among marine filter feeders in a soft-sediment environment. *Ecology*. 61:129-139.
39. PRICE, R. J., and J. S. LEE. 1972. Paralytic shellfish poison and melanin distribution in fractions of toxic butter clam (*Saxidomus giganteus*) siphon. *Journal of the Fisheries Research Board of Canada*. 29:1657-1658.
40. RICKETTS, E. F., and J. CALVIN. 1952. Between Pacific tides : an account of the habits and habitats of some five hundred of the common, conspicuous seashore invertebrates of the Pacific Coast between Sitka, Alaska, and Northern Mexico. Stanford : Stanford University Press, Stanford.
41. —. 1971. Between Pacific tides. Stanford University Press, Stanford, California.
42. ROBINSON, A. M., and W. P. BREESE. 1982. The spawning season of four species of clams in Oregon. *Journal of Shellfish Research*. 2:55-57.

43. SCHANTZ, E. J., V. E. GHAZAROSSIAN, H. K. SCHNOES, F. M. STRONG, J. P. SPRINGER, J. O. PEZZANITE, and J. CLARDY. 1975. Structure of Saxitoxin. *Journal of the American Chemical Society*. 97:1238-1239.
44. SHIMAMOTO, M. 1986. SHELL MICROSTRUCTURE OF THE VENERIDAE BIVALVIA AND ITS PHYLOGENETIC IMPLICATIONS. *Science Reports of the Tohoku University Second Series (Geology)*. 56:1-39.
45. SMOLOWITZ, R., and G. DOUCETTE. 1995. Immunohistochemical localization of Saxitoxin in the siphon epithelium of the butter clam, *Saxidomus giganteus*. *Biological Bulletin*. 189:229-230.
46. VALE, P. 2010. New saxitoxin analogues in the marine environment: developments in toxin chemistry, detection and biotransformation during the 2000s. *Phytochemistry Reviews*. 9:525-535.
47. WALNE, P. R. 1973. Growth rates and nitrogen and carbohydrate contents of juvenile clams, *Saxidomus giganteus*, fed three species of algae. *Journal of the Fisheries Research Board of Canada*. 30:1825-1830.

Updated 2016

Phoronida

Phoronis pallida

Phylum: Phoronida
Family: Phoronidae

A lophophorate coelomate

Description

Size—one of the smaller phoronids: 15-30 mm long (Silen 1954): sp. *pallida*. Sand covered tube just a little larger (Silen 1952); expanded animal can be 25% longer than tube.

Color—trunk pale, white, posterior end light red. Internal organs visible as red (contain hemoglobin (Zimmer and Haderlie 1980). Tentacles white, without pigmented amoebocytes: sp. *pallida* (Silen 1954). Larva opaque yellow, tube yellow to brown-red (from secreted matter) (Silen 1954).

Trunk—wormlike: un-segmented, smooth and soft, but faintly annulated (Hyman 1959), no setae - all characteristic of phylum Phoronida. Can be faintly differentiated into several zones: sp. *pallida* (Silen 1954). Trunk and whole tube curved toward anal side (Silen 1954) (fig. 6).

Lophophore—a horseshoe-shaped extension of the mesosome (Hyman 1959); includes mouth and consists of a crown of tentacles. Number of lophophore spirals, number of tentacles characteristic of sp. *pallida* - a single row of 50-140 tentacles, in a simple spiral (Emig 1974)(fig. 3).

Tentacles—straight, finger-shaped: Phoronida (Zimmer and Haderlie 1980); not threadlike (fig. 2a). In *P. pallida* there can be 50-140, but usually around 50 (Zimmer and Haderlie 1980), sometimes more (S.F. Bay specimens). Tentacles can be regenerated (MacGinitie and MacGinitie 1949).

Anus—dorsal to mouth (Hyman 1959); digestive tract U-shaped (fig. 2).

Nephridiopores—lateral to anus (fig. 2): excretory and for emission of sex cells (Hyman 1959).

Collar—not present at base of lophophore: genus *Phoronis* (Zimmer 2007) (figs. 1, 2, 3). Lophophore base and trunk demarcation a slight groove; collar, (if present, as in genus *Phoronopsis*), extends all around trunk. (Do not confuse anus and nephridiopores on dorsal base of lophophore with a true collar.)

Bulb—(ampulla)-enlarged posterior end (fig. 1).

Internal Structure—much systematic work based on longitudinal muscle patterns, etc., not easily studied by casual field worker. *P. pallida* muscles have unusual longitudinal and circular patterns, and few bundles of muscles (18-19). Giant nerve fibers found in this phylum - except in *P. ovalis* - also vary in size and number. *P. pallida* has one giant nerve fiber, on the left side - usual position in phylum (Emig 1974). Nephridial structure is also important in systematics.

Tube—separate, vertical, chitinous, covered with thin layer of sand grains. Membranous distally (Zimmer 2007). Distinctly flexed 1/3 of way to base: sp. *pallida* (Silen 1954) (fig. 6). Tube flexible, tough, can't be easily broken. Basal end of tube open.

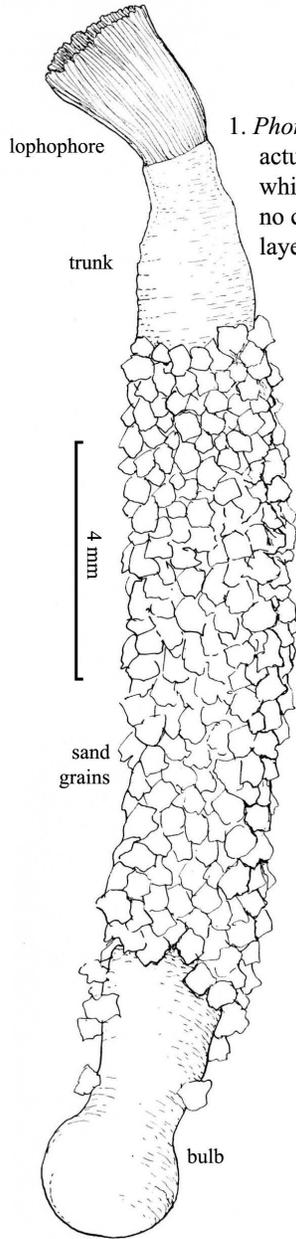
Larva—actinotroch (from which this species was first described (Schneider 1862)) is small: 0.6 mm long, active; found on water's surface. Mature larva found on substrate, has 5 pairs of tentacles (Silen 1954) (fig. 5). Young actinotrochs are photopositive and planktotrophic (Silen 1954).

Possible Misidentifications

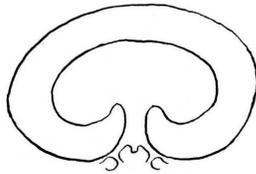
Phoronids are worm-like, with an unsegmented, though slightly annulated trunk and a crown of tentacles on the anterior end. Some polychaetes also have this general form. Phoronids, however, have no setae or segmentation on their trunks. Phoronid tentacles are straight and finger-like, not branched or thread-like, as in polychaetes. The phoronid lophophore is circular-crescent shaped or a double spiral.

Only 2 genera of Phoronida and probably fewer than 20 species are known worldwide. Many of these can be found on the Pacific coast, but only 3 are common intertidally: *Phoronopsis harmeri*, *Phoronis vancouverensis*, and *P. pallida*. The main population of each of these species is likely subtidal (Zimmer 2007).

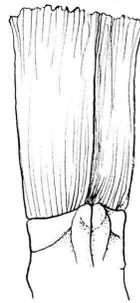
Phoronopsis spp. can be distinguished from *Phoronis* spp. by the presence in the



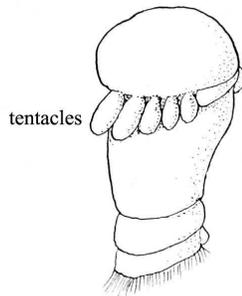
1. *Phonois pallida* x100:
actual size 20 x 2mm; lophophore of c. 50
white tentacles; trunk white, unsegmented;
no collar at base of lophophore; tube a single
layer of sand grains.



3. Schematic, lophophore:
dorsal view; a simple spiral
(from Emig 1971).

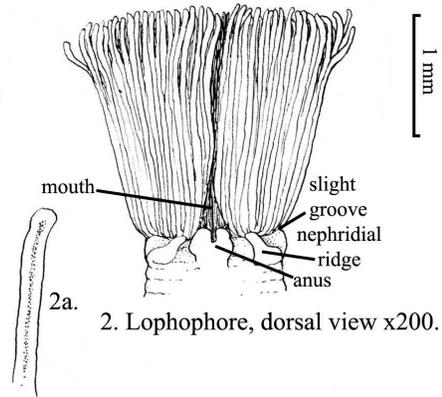


4. Lophophore, *Phoronopsis harmeri*:
epidermal collar at base of lophophore
(from Emig 1974).

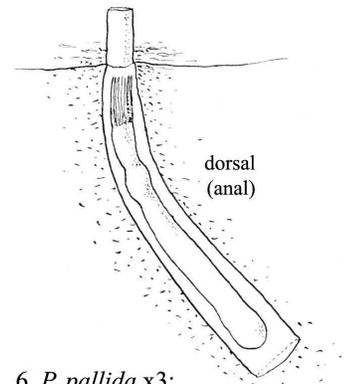


5. Actinotroph (L: 0.6mm) x100:
mature larva: 5 pairs tentacles
(from Silen 1954).

Phoronis pallida



2. Lophophore, dorsal view x200.



6. *P. pallida* x3:
withdrawn into tube; tube flexed
1/3 of way to base, toward anal side;
bottom of tube open
(from Silen 1952).

former of a collar at the base of the lophophore, lacking in *Phoronis* spp. The three Pacific representatives of this genus include:

Phoronopsis harmeri Pixell, 1912 (senior synonym of *P. viridis* (Hilton, 1930), a large common phoronid often found in great masses on the mudflats. Individuals can be green or white and up to 200 mm long, with up to 300 green tentacles with white spots (Hyman 1959, Zimmer 2007). *P. harmeri* is usually larger than *P. pallida* (up to 60 mm long), and has a collar, as in all *Phoronopsis* spp. It is also found in the Atlantic (Azores). This species is abundant on Oregon and Washington tidal flats, and is largely distinguished from *P. pallida* by its size, color and its collar.

P. pacifica (Torrey, 1901), found first in Humboldt Bay, and described from Puget Sound as well, is also considered a synonym of *P. harmeri* (Emig 1974).

The third *Phoronopsis* species, *P. californica* Hilton, 1930, is probably limited to southern California. It has a large bright orange lophophore with elaborate spirals; it is solitary, and can be up to 12" (300 mm) long (MacGinitie and MacGinitie 1949).

There are four other species of *Phoronis* reported from our coast:

P. architecta Andrews, 1890 is an Atlantic species, also found subtidally from southern California to British Columbia, and occasionally intertidally (Zimmer and Haderlie 1980). Its lophophore is flesh-colored, or rarely reddish, with white bands and flecks. It has no collar, (like *P. pallida*), but is 2x the size of the latter; its sand encrusted tube is straight, not flexed.

P. psammophila has been synonymized with *P. architecta* (Emig 1982). *P. ovalis* Wright, 1856 is much smaller even than *P. pallida*, (only 6 mm long). It bores in shell and limestone and is not found living freely in the mud.

P. vancouverensis Pixell, 1912 (now senior synonym of *P. ijimai* Oka, 1897) is whitish, like *P. pallida*. It is larger, however, 20-50 mm long, and has 72-100 tentacles (average 90 according to Pixell, 1912), and grows in intertwined clusters of great density, often on pilings and on rocks. Its tubes are covered with detritus, not sand grains.

P. hippocrepia (Wright), the European species, is considered to be separate from *P. vancouverensis* above (Emig 1971).

Ecological Information

Range—Scandinavia; Pacific coast of North America.

Local Distribution—Coos Bay: Charleston mudflats.

Habitat—in soft sand, muddy sand (Emig 1974); on intertidal mudflats. Commensal in *Upogebia pugettensis* burrows (Zimmer 2007)

Salinity—all phoronids are marine (Zimmer and Haderlie 1980). Only one species, *P. euxinicola*, is found in brackish water, in the Black Sea (Hyman 1959). These specimens collected at 30 ‰ (Coos Bay).

Temperature—phoronids are found in shallow waters of tropical and temperate ranges (Hyman 1959); most are temperate (Zimmer 1980). Some can regenerate after extremes of weather have left only fragments in tubes: in winter (Italy) and summer (Japan) (Hyman 1959).

Tidal Level—intertidal, also subtidal at a number of locations worldwide (Zimmer 2007) down to 12m deep (Emig 1974). (Other phoronids can be found down to 140m.)

Associates—commensal in burrows of *Upogebia pugettensis*, though not often found with the sympatric mud shrimp *Neotrypaea californiensis* (Zimmer 2007).

Quantitative Information

Weight—

Abundance—

Life History Information

Reproduction—a simultaneous hermaphrodite: eggs and sperm extruded into body cavity from reproductive organs, fertile eggs expelled into seawater via nephridiopores (MacGinitie and MacGinitie 1949). In some species, larvae live among tentacles of adult female, but not in *P. pallida*, which lacks nidamental (nesting) organs (Emig 1974). No asexual propagation, although regeneration of crown of tentacles possible (Silen 1952). Eggs laid on 2 - 3 successive summer nights (Sweden), 28 at a time (Silen 1954).

Growth Rate—fertilized egg immobile for 20 hours; to blastula stage in 20 hours more. After gastrulation begins, hood develops; in 25-30 more hours, a ciliated ridge appears,

becoming the crown of tentacles. First tentacles show after two days. (Growth stopped in lab after six days (Silen 1954). The actinotroch progresses from four tentacles to metamorphosis in 12-14 days. It is active and moves quickly horizontally and vertically - dives, floats, and rushes. Details of larval development and phylogenetic implications are given by Santagata (2004a) and a key to larval stages is available in Shanks (2001). Mature larvae are photonegative; pre-settlement behavior is induced by a waterborne cue from *Upogebia pugettensis*, a shrimp species with which *P. pallida* is commensal (Santagata 2004b).

Metamorphosis is triggered by presence of proper substrate (mud, sand), and takes 15 minutes. The actinotroch takes a horizontal position, ventral side down, then evaginates metasomal sac. The transition is made from control by the larval neuromuscular system to that of the juvenile, resulting in the apoptosis of larval structures. This succession of events suggests lophotrochozoan affinities (Santagata 2002). Finally, a thin tube is formed, and the worm begins to burrow.

Longevity—

Food—all phoronids are ciliary mucus feeders, gathering suspended particles by tentacular currents (Hyman 1959). Actinotrochs eat peridinians, not diatoms (Silen 1952).

Predators—

Behavior—movement limited to emergence from anterior end of tube, and expansion of crown (in undisturbed conditions), and to withdrawal into tube if disturbed (Hyman 1959). Adults not light sensitive (Hyman 1959).

Bibliography

1. EMIG, C. C. 1971. Remarques sur la systématique des Phoronidea. *Marine Biology*. 8:154-159.
2. ———. 1974. The systematics and evolution of the phylum Phoronida. *Journal of Zoological Systematics and Evolutionary Research*. 12:128-151.
3. EMIG, C.C. 1982. The biology of Phoronida. *Advances in Marine Biology*. 19: 1-89.
4. HYMAN, L. H. 1959. *Invertebrates: Smaller coelomate groups*. McGraw-Hill, New York.

5. MACGINITIE, G. E., and N. MACGINITIE. 1949. *Natural history of marine animals*. McGraw-Hill Book Co., New York.
6. PIXELL, H. L. M. 1912. Two new species of the Phoronidea from Vancouver Island. *Quarterly Journal of Microscopical Science*. 58:257-284.
7. SANTAGATA, S. 2002. Structure and metamorphic remodeling of the larval nervous system and musculature of *Phoronis pallida* (Phoronida). *Evolution & Development*. 4(1): 28-42.
8. ————— 2004a. Larval development of *Phoronis pallida* (Phoronida): Implications for morphological convergence and divergence among larval body plans. *Journal of Morphology*. 259: 347-358.
9. ————— 2004b. A waterborne cue for the actinotroch larva of *Phoronis pallida* (Phoronida) produced by *Upogebia pugettensis* (Decapoda: Thalassinidea). *Biological Bulletin*. 207(2): 103-115.
10. SCHNEIDER, A. 1862. Über die Metamorphose der Actinotrocha branchiata. *Archiv für Anatomie und Physiologie*:47-65.
11. SHANKS, A.L. 2001. An identification guide to the larval marine invertebrates of the Pacific northwest. Oregon State University Press, Corvallis, OR.
12. SILEN, L. 1952. Researches on Phoronidea of the Gullmar Fiord Area (West coast of Sweden). *Arkiv för Zoologi*. 4:95-140.
13. ———. 1954. Developmental biology of Phoronidea of the Gullmar Fiord area (West coast of Sweden). *Acta Zoologica*. 35:215-257.
14. ZIMMER, R. L. 2007. Phylum Phoronida, p. 860-863. *In: Light's manual; intertidal invertebrates of the central California coast*. J. T. Carlton (ed.). U.C.Press, Berkeley.
15. ZIMMER, R. L., and E. C. HADERLIE. 1980. Chapter 7: Brachiopoda and Phoronida, p. 108-116. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, California.

Updated 2014
K. Meyer

Echinodermata

Pisaster brevispinus

The pink, short-spined sea star

Phylum: Echinodermata
Class: Asteroidea
Order: Forcipulatida
Family: Asteriidae

Taxonomy: The genus *Pisaster* includes three Pacific coast sea star species, including *Pisaster brevispinus*. One can find many historic synonyms for *P. brevispinus*, including *P. papulosus* and *P. paucispinus*. Furthermore, two subspecies were erected for *P. brevispinus* in 1930 (Fisher) but the morphological and genetic status of these subspecies is currently unknown. Before being assigned to the genus *Pisaster*, this species belonged to the, currently accepted, genus *Asterias* (synonyms *A. brevispina*, *A. papulosa*).

Description

Size: One of the largest asteroids worldwide and typically 320 mm in diameter (Hyman 1955; Feder 1980; Mah 2007; see <http://echinoblog.blogspot.com/2008/06/giant-pink-monsters-among-us-enter.html>), with largest reported size 900 mm (Mah and Blake 2012). The illustrated specimen (from Coos Bay) is 190 mm in diameter.

Color: Oregon specimens always pink, although some keys indicate gray-green or maroon-purple mottling (see Plate 25, Kozloff 1993).

General Morphology: Sea stars (Asteroidea) are conspicuous members of the intertidal and subtidal. Their bodies are composed of a **central disc** from which arms or **rays** extend. The star-shaped body can be divided into an **oral** (or ventral) side where the mouth is located and **aboral** (or dorsal) side.

Body: Body is firm, not weak and flabby.

Rays: Five, unless damaged. Each ray is tapering and most broad where they join the central disc, but not broad enough to give webbed appearance (as in *Patiria* spp.).

Central Disc: Large, raised, but not set off from arms or distinctly disc-like as in Ophiuroidea (brittle stars). Contains (conspicuous) madreporite (Figs. 1, 3) and (less conspicuous) anus.

Aboral Surface: Aboral surface rough and spiny in texture and pink in color.

Spines: Short (“brevi”, shorter than other *Pisaster* species, Feder 1980), spines do not usually form reticulated pattern or crescentic arcs and there is at least one straight row of spines down each arm (Fig. 1). Spines occur singly or in small groups of two and three (up to five) and are separated by areas of soft tissue (Fig. 3). Large spines are often shaped like onion domes. The spines in the center of the disc do not form a distinct star (Fig. 1).

Madreporite: The madreporite, which filters water into the interior stone canal, is raised, with channels, and is a conspicuous plate on the central disc (Fig. 1).

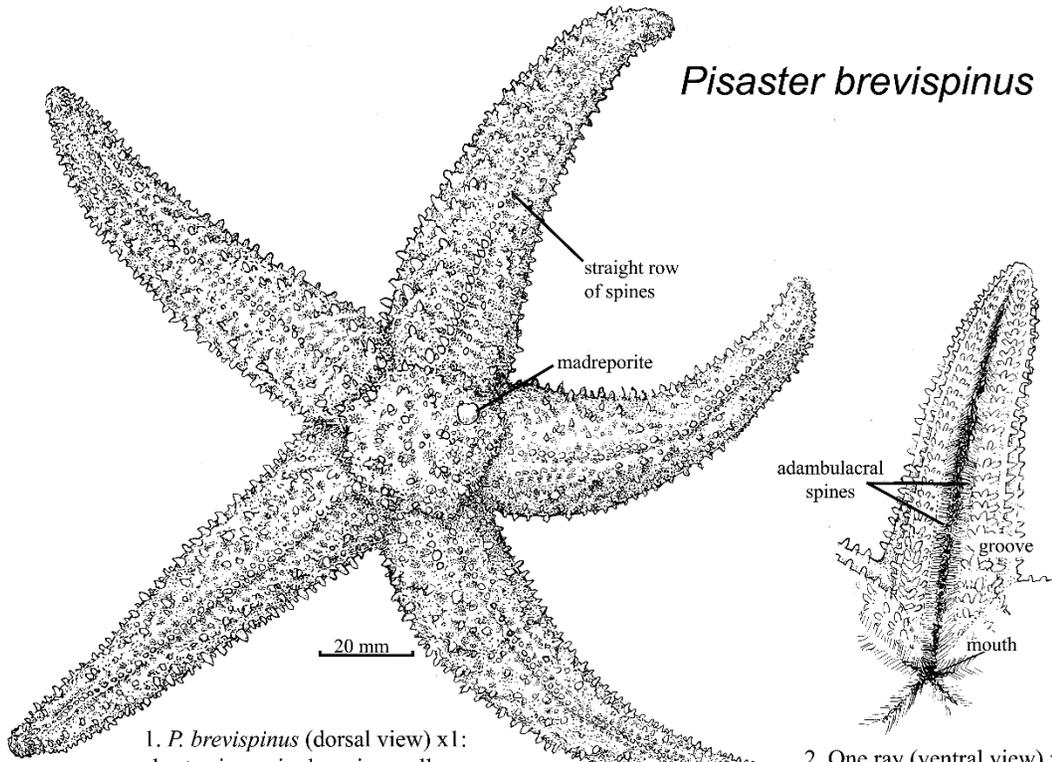
Pedicellariae: Stalked or sessile appendages with pincers, used for removing invaders. Pedicellariae are bird beak-like and two-jawed in *Pisaster* species. Very small pedicellariae cluster around spines (Fig. 3) and no large sessile pedicellariae are visible. Used in deterring predators (e.g. *Solaster dawsoni*, Van Veldhuizen and Oakes 1981).

Anus: Inconspicuous and near center of aboral surface.

Oral Surface: Oral surface ochre in color and consists of hard, textured surface from extension of aboral surface and ambulacral grooves running the length of each arm and converging at the mouth. Grooves are fleshy in texture due to the presence of tube feet.

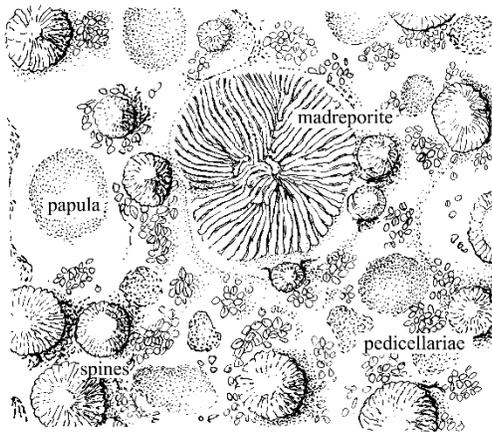
Spines: Four rows of flattened (elliptical) blunt spines with small clustered pedicellariae at their bases and one row of long thin spine-like ambulacral spines (Fig. 4). A few clusters of pedicellariae occur at the bases of these spines, but there are no pedicellariae on the spines (Fisher 1930; Hyman 1955).

Pisaster brevispinus

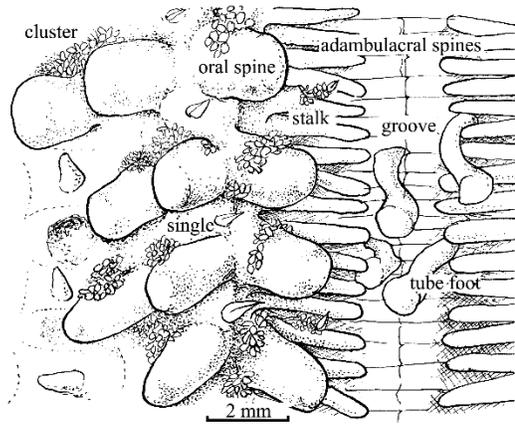


1. *P. brevispinus* (dorsal view) x1:
short spines, single or in small groups; a
straight row down each arm; soft tissue between
spines; pink color; five tapering arms; large raised central disc.

2. One ray (ventral view) x1:
adambulacral groove with
tube feet.



3. Dorsal spines, madreporite x8:
spines short, some "onion domed" or in small
groups; rounded madreporite; pedicellariae
small, clustered; dark papulae.



4. Ventral spines, groove x8:
oral spines blunt, elliptical; adambulacral
spines along groove; pedicellariae clustered,
single or stalked.

Mouth: Large and at center of ventral surface (Fig. 2).

Pedicellariae: Two types of pedicellariae on the oral surface: (1) Small and clustered around bases of oral spines, and (2) large stalked pedicellariae on bases of adambulacral spines (Fig. 4).

Tube Feet: Used in locomotion and part of vascular system. Present on the ventral side in four rows that are staggered down each ambulacral groove (Fig. 4).

Ambulacral grooves: Grooves are long furrows on oral surface of arms, which contain tube feet and are lined with adambulacral spines (Fig. 4).

Possible Misidentifications

Among the large five-armed sea stars, *Pisaster* species are noted for their thick arms, low papillate dorsal spines and pedicellariae. *Pisaster brevispinus* is readily identifiable by its pink coloration, its seemingly soft appearance, and its unusual (for sea stars) occurrence on soft substrates. Two other Asteroidea species share these characteristics, but can be differentiated as follows: (1) *Evasterias troschelii* is slender like *P. brevispinus*, but is generally orange-red or blue-gray (in Coos Bay), not pink. Its clusters of oral pedicellariae are on the adambulacral spines, not just at their bases as in *P. brevispinus* (Fig. 4). Like *P. brevispinus*, *E. troschelii* is subtidal (Ricketts and Calvin 1971; Mah 2007) and its preferred range is in Puget Sound, Washington, although it is known to northern California. (2) *Orthasterias koehleri* has large, sharp dorsal spines, each surrounded by a distinct ring of large pedicellariae. These spines are arranged in distinct radial rows and *O. koehleri* is often red with yellow mottling (Mah 2007).

Two other species of *Pisaster* can be found locally: (1) *Pisaster ochraceus* is a common coastal sea star, and is only present in lower reaches of high salinity estuarine systems. It is red, brown, or ochre (juveniles are gray), never pink. It inhabits only hard substrates (e.g. rocks, pilings), not soft sand. The dorsal spines on *P. ochraceus* form reticulated patterns and the straight line(s) of spines down each arm

that are typical of *P. brevispinus* are absent from *P. ochraceus*. (2) *Pisaster giganteus* is bluish gray, with blunt, clubbed dorsal spines, each surrounded by a ring of blue flesh around which is a ring of pedicellariae. *Pisaster giganteus* is a low intertidal sea star, and usually found further south than Oregon. In spite of its name, it is smaller than *P. brevispinus* when fully grown (Mah 2007).

Sea stars are extremely variable intra-specifically. Fisher describes two forms of *P. brevispinus* (with status currently unknown): (1) *P. b. brevispinus*, from Puget Sound, Washington to Crescent City, California with an abundance of aboral spines (Fisher 1930). These spines are in large groups, up to 10 and can form radial bands; (2) *Pisaster brevispinus pacispinus* has few spines, standing singly or in groups of two and three. The spines are usually stout with subconical acorn-shaped with grooved tips. Papillae (respiratory surfaces) are numerous and conspicuous in this form (Fig. 3).

Ecological Information

Range: Type locality is San Francisco Bay, California (Ahearn 1995). Sitka, Alaska, to Santa Barbara, California (Fisher 1930).

Local Distribution: Typically offshore and on sand bottoms and also found in channel bottoms of large estuaries, like Coos Bay.

Habitat: Only in quietest waters and also on wharf pilings and rocks. Cannot tolerate exposure to air or to low salinities for extended periods (Ricketts and Calvin 1971).

Salinity: Collected at salinities around 30.

Temperature: Cold to temperate. Does not tolerate aerial exposure as well as *P. ochraceus* (Feder 1980).

Tidal Level: Present in low intertidal, but most common subtidally from 0.5–100 m (Feder 1980).

Associates: On low pilings, associates include the congener, *P. ochraceus*, as well as the anemone *Metridium*, and tunicates, mussels and barnacles. Several incidences of sudden sea star die off have occurred since 1972, but the most recent to the northwest coast of North America began in June 2013 and is called sea star wasting disease. Affected individuals have ectodermal lesions and tissue decay that eventually leads to death (within 2–3 days).

The water-vascular system loses the ability to maintain hydrostatic pressure and individuals often look flaccid when infected. Increased temperature further heightens infection intensities (Bates et al. 2009). The current die off of sea stars is the most significant due to its widespread geographic range and large number of species infected (Hewson et al. 2014). Recently, researchers determined this disease is most likely associated with a family of single stranded DNA viruses (densovirus, *Parvoviridae*) and is now called sea star-associated densovirus (SSaDV). Incidentally, this same virus was detected in museum specimens and, thus, may have been present on the Pacific coast and undetected since those specimens were collected in 1942. Although the specific pathogen is not known in certainty, SSaDV is currently the most likely candidate (Hewson et al. 2014).

Abundance: Occasional and not as common as *P. ochraceus* (Feder 1980).

Life-History Information

Reproduction: Forcipulate asteroids primarily have separate sexes and free-swimming planktonic larvae (Fisher 1930; Chia et al. 1987). *Pisaster* species do not brood their eggs or young as do some Asteroidea, e.g. *Leptasterias* (Sutton 1975). Many species can be induced to spawn and are routinely used in developmental research (e.g. *P. ochraceus*). One pair of gonads is present in each arm and, when spawning, sea stars lift and suspend their body with their arms and gametes are released through gonopores on the aboral surface (Chia et al. 1987). Ten gonads are like feathery tufts, two in each ray, and occur next to the central disc in *P. brevispinus*. The spawning period is from March to August (San Juan Islands, Washington, Chia et al. 1987) and April in Monterey, California (Feder 1980; Miller 2001). Reproductive cycle much like that of *P. ochraceus* where development proceeds as follows (12°C): 2 cells at 5hr, 4 cells at 6hr, 8 cells at 7hr, hatching at 29–32 hr, gastrula at 44–63 hr, planktotrophic bipinnaria larva at 5d post fertilization (Chia et al. 1987).

Larva: Embryos develop into planktotrophic larvae called bipinnariae (Chia et al. 1987; Miller 2001). Bipinnaria larvae are easily recognizable in the plankton (Fig. 26.1, 26.2, Chia et al. 1987), they are large, fleshy and uniformly ciliated with a distinct, continuous

ciliated band that is used for feeding and swimming. They have a large mouth, esophagus, intestine and anus. They can have many long arms, increasing in number with age and can become long and floppy (Fig. 3, Miller 2001). The juvenile sea star develops from the left posterior portion of the larval body. Late stage bipinnaria develop three arms (called brachiolar arms) and a central adhesive disc, anteriorly. Larvae at this stage are called brachiolaria (see Fig. 4, Miller 2001) and they use these arm to attach to substratum at metamorphosis.

Juvenile:

Longevity:

Growth Rate:

Food: Feeds on a variety of invertebrates including clams, snails, mussels, barnacles sand dollars as well as scavenging dead or dying fish or squid. The stomach of individuals can be extended up to 8 cm to digest prey externally (Feder 1980). Can apparently sense and dig out clams (e.g. *Saxidomus*, *Protothaca*) from gravel (Smith 1961; Feder 1980) and includes more clams in its diet than does *P. ochraceus* (Mauzey et al. 1968). *Pisaster brevispinus* can also extend tube feed into the sediment to considerable depths (roughly equal to arm length, up to 20 cm, Van Veldhuizen and Phillips 1978; Feder 1980; see <http://echinoblog.blogspot.com/2008/06/giant-pink-monsters-among-us-enter.html>) to seek out prey. Sand dollars escape by quickly burying themselves when *P. brevispinus* appears (MacGinitie and MacGinitie 1949).

Predators: Sea otters (McCleneghan and Ames 1976) and other sea stars (e.g. *Solaster dawsoni*, Van Veldhuizen and Oakes 1981), although their large size usually reduces predation.

Behavior: *Pisaster brevispinus* and, the sunflower star, *Pycnopodia helianthoides* are known to compete and fight for food (Wobber 1975; Feder 1980). A significant escape response was observed for *P. brevispinus* from both *P. helianthoides* and *S. dawsoni* (Van Veldhuizen and Oakes 1981).

Bibliography

1. AHEARN, C. G. 1995. Catalog of the type specimens of seastars (Echinodermata: Asteroidea) in the National Museum of Natural History,

- Smithsonian Institution. Smithsonian Contributions to Zoology. 572:1-59.
2. BATES, A. E., B. J. HILTON, AND C. D. G. HARLEY. 2009. Effects of temperature, season and locality on wasting disease in the keystone predatory sea star *Pisaster ochraceus*. *Diseases of Aquatic Organisms*. 86:245-251.
 3. CHIA, F., L. R. MCEDWARD, R. L. MILLER, T. E. SCHROEDER, R. L. SHIMEK, S. T. SMILEY, AND R. STRATHMANN. 1987. Phylum Echinodermata, Class Asteroidea, p.535-555. *In: Reproduction and development of marine invertebrates of the northern Pacific coast*. M. F. Strathmann (ed.). University of Washington Press, Seattle, WA.
 4. FEDER, H. M. 1980. Asteroidea: the sea stars, p. 117-135. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
 5. FISHER, W. K. 1930. Asteroidea of the north Pacific and adjacent waters. *Bulletin of the United States Natural Museum*. 76.
 6. HEWSON, I., J. B. BUTTON, B. M. GUDENKAUF, B. MINER, A. L. NEWTON, J. K. GAYDOS, J. WYNNE, C. L. GROVES, G. HENDLER, M. MURRAY, S. FRADKIN, M. BREITBART, E. FAHSBENDER, K. D. LAFFERTY, M. A. KILPATRICK, M. C. MINER, P. RAIMONDI, L. LAHNER, C. S. FRIEDMAN, S. DANIELS, M. HAULENA, J. MARLIAVE, C. A. BURGE, M. E. EISENLORD, AND D. C. HARVELL. 2014. Densovirus associated with sea-star wasting disease and mass mortality. *Proceedings of the National Academy of Sciences of the United States of America*. 111:17278-17283.
 7. HYMAN, L. H. 1955. *The Invertebrates: Echinodermata*. McGraw-Hill, New York.
 8. KOZLOFF, E. N. 1993. *Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia*. University of Washington Press, Seattle, WA.
 9. MACGINITIE, G. E., AND N. MACGINITIE. 1949. *Natural history of marine animals*. McGraw-Hill Book Co., New York.
 10. MAH, C. 2007. Echinodermata: Asteroidea, p. 922-930. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. Fourth edition, completely revised and expanded. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
 11. MAH, C. L., AND D. B. BLAKE. 2012. Global diversity and phylogeny of the Asteroidea (Echinodermata). *Plos One*. 7:DOI: 10.1371/journal.pone.0035644.
 12. MAUZEY, K. P., A. C. BIRKELAND, AND P. K. DAYTON. 1968. Feeding behavior of asteroids and escape responses of the prey in the Puget Sound region. *Ecology*. 49:603-619.
 13. MCCLENEGHAN, K., AND J. A. AMES. 1976. Unique method of prey capture by a sea otter, *Enhydra lutris*. *Journal of Mammalogy*. 57:410-412.
 14. MILLER, B. A. 2001. Echinodermata, p. 270-290. *In: An Identification guide to the larval marine invertebrates of the Pacific Northwest*. A. L. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 15. RICKETTS, E. F., AND J. CALVIN. 1971. *Between Pacific tides*. Stanford University Press, Stanford, California.
 16. SMITH, L. S. 1961. Clam-digging behavior in the starfish, *Pisaster brevispinus* (Stimpson, 1857). *Behavior*. 18:148-153.
 17. SUTTON, J. E. 1975. Class Asteroidea, p. 623-627. *In: Light's manual: intertidal invertebrates of the central California coast*. S. F. Light, R. I. Smith, and J. T. Carlton (eds.). University of California Press, Berkeley.
 18. VANVELDHUIZEN, H. D., AND V. J. OAKES. 1981. Behavioral responses of seven species of asteroids to the asteroid predator, *Solaster dawsoni*. *Oecologia*. 48:214-220.
 19. VANVELDHUIZEN, H. D., AND D. W. PHILLIPS. 1978. Prey capture by *Pisaster brevispinus* (Asteroidea,

- Echinodermata) on soft substrate.
Marine Biology. 48:89-97.
20. WOBBER, D. R. 1975. Agonism in
asteroids. Biological Bulletin. 148:483-
496.

Updated 2015

T.C. Hiebert and K. Meyer

Pisaster ochraceus

Common Pacific sea star, ochre sea star, purple sea star

Phylum: Echinodermata
Class: Asteroidea
Order: Forcipulatida
Family: Asteriidae

Taxonomy: The genus *Pisaster* includes three Pacific coast sea star species, including *Pisaster ochraceus*. One can find many historic synonyms for *P. ochraceus*, including *P. confertus* and *P. fissispinus* for this species, but they are not currently used. Furthermore, two subspecies were erected for *P. ochraceus* in 1996 (Clark) but morphological and genetic data does not support this designation and, instead, recognizes the single species *P. ochraceus* (Stickle et al. 1992; Lambert 2000; Frontata-Uribe et al. 2008). Before becoming a member of the genus *Pisaster*, this species belonged to the, currently accepted, genus *Asterias* (synonyms *A. ochracea*, *A. fissispina*, *A. ianthina*, *A. janthina*, *A. margaritifera*) or the former genus *Asteracanthion* (now *Asterias*).

Description

Size: Average size (Monterey, California) is 140 mm in diameter, where each ray (arm) is 40 mm in length (Fisher 1930). The illustrated specimen is 150 mm in diameter. Puget Sound specimens are regularly 250 mm in diameter (Kozloff 1993). Weight ranges (wet weight) from 37.8–8.34 g (28 animals, Feder 1970).

Color: Aboral (dorsal) surface red, purple, brown or ochre (especially on open coast) (see Plate 25, Kozloff 1993). Specimens most commonly purple (Puget Sound, Washington). Oral (ventral) surface ochre. Juveniles gray with brown aboral patches (Feder 1970). Body color may vary with geographic region. Harley et al. (2006) found more brown (68–90%) and orange (6–28%) individuals in Washington (Olympic Peninsula), Oregon and California but more (95%) purple individuals in British Columbia and Puget Sound, Washington. This variation in color could be due to the predominating food source for *P. ochraceus* in the two regions, where mussels are more common in Washington, Oregon and California but barnacles are the most common food source in British Columbia and Puget Sound sites

(Harley et al. 2006; see also <http://echinoblog.blogspot.com/search/label/Pisaster%20ochraceus>).

General Morphology: Sea stars (Asteroidea) are conspicuous members of the intertidal and subtidal. Their bodies are composed of a **central disc** from which arms or **rays** extend. The star-shaped body can be divided into the **oral** (or ventral) side where the mouth is located and **aboral** (or dorsal) side.

Body: Stiff body morphology that is hard to the touch.

Rays: Five rays (unless damaged, can range from four to seven rays, Feder 1980). Each ray is tapering, thick, large, not sharply demarcated from disc and broadest where they join the central disc (Dyakonov 1950), but not broad enough to give webbed appearance (as in *Patiria* spp.).

Central Disc: Large, convex, arched, not distinct or as disc-like as in Ophiuroidea (brittle stars). Contains (conspicuous) madreporite (Figs. 1, 3) and (less conspicuous) anus. Diameter of disc less than 1/3 body diameter.

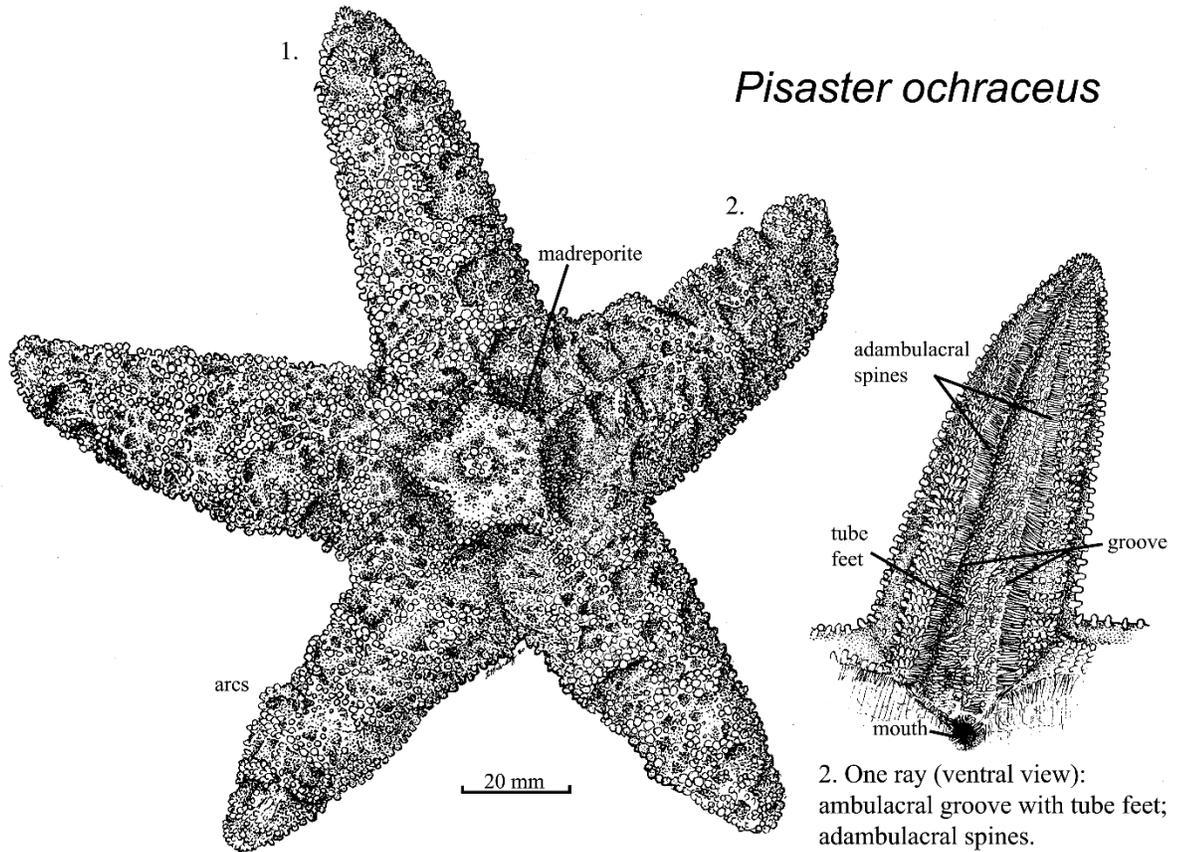
Aboral Surface: Aboral surface rough in texture and red, purple, brown or ochre in color.

Spines: Low, small, serrated, rounded, bead-like or papillate (Figs. 1, 3). Spines form crescentic arcs at arm tips. No straight mid-dorsal row of arm spines. Spines in center of disc form a distinct star in the illustrated specimen (Fig. 1). Two types of spines include: (1) small, clustered around dorsal spines and (2) a few solitary, large, sessile pedicellariae scattered over dorsal surface (Fig. 3).

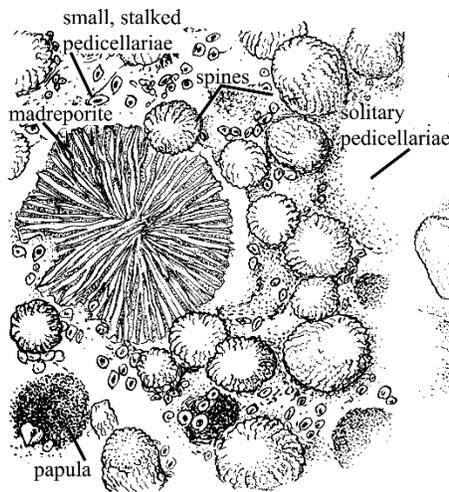
Madreporite: A sieve-like structure which serves as the water intake into the stone canal is conspicuous about 1/3 of radius from center of disc (Fig. 1, between arms numbered 1 and 2).

Pedicellariae:

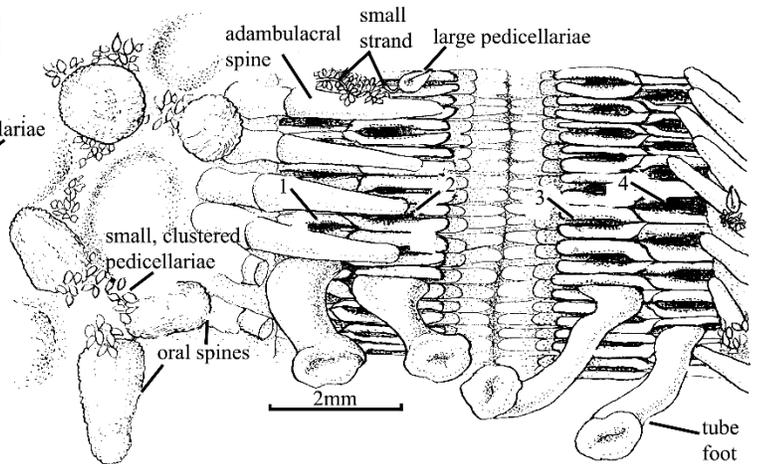
Pisaster ochraceus



1. *Pisaster ochraceus* (dorsal view) x1:
stiff, harsh surface; reticulated pattern, spines in arcs;
five thick, tapering arms; large arched central disc.



3. Madreporite, dorsal spines x12:
madreporite large, flat, filter-like;
dorsal spines short, rounded, bead-like;
pedicellariae stalked, small, clustered;
sessile, large, solitary.



4. Ambulacral groove (ventral view) x12:
all tube feet removed except four, to show four rows across groove;
adambulacral spines along groove; pedicellariae small, clustered
on expandable strands; small and clustered at
bases of oral spines.

Anus: Inconspicuous, near center of aboral surface and is surrounded by small pedicellariae.

Oral Surface: Oral surface ochre in color and consists of hard, textured extension of aboral surface and ambulacral grooves running the length of each arm and converging at the mouth. Grooves are more fleshy in texture from presence of tube feet.

Spines: Spines serrated, blunt, heavy and more spine-like than bead-like (Fig. 4). Adambulacral spines (lining ambulacral grooves) are articulated, long, thin (Fig. 4). Three types of spines ventrally: (1) small, clustered around bases of oral spines (Fig. 4); (2) small pedicellariae clustered on expandable strands between adambulacral spines (Fig. 4); and (3) large pedicellariae on these same strands (Fig. 4). There are no pedicellariae on the adambulacral spines (*Pisaster*, Fisher 1930; Hyman 1955).

Mouth: Large, in center of disc (Fig. 2). *Pisaster* species can extrude the stomach through this opening, engulfing food and initiating digestion externally (Feder 1980).

Pedicellariae: Stalked or sessile appendages used for removing invaders (e.g. barnacles larvae) or deterring predators (e.g. *Leptasterias hexactis*, Wobber 1975; *Solaster dawsoni*, Van Veldhuizen and Oakes 1981). Pedicellariae are bird beak-like and two-jawed in *Pisaster* species.

Tube Feet: Used in locomotion and part of water vascular system. Present on ventral side in ambulacral grooves where they are staggered in pairs, four rows across and down each ambulacral groove (Fig. 4).

Ambulacral grooves: Grooves are long furrows on oral surface of arms, which contain tube feet (Figs. 2, 4) (Booolootian 1966). Along each edge of groove are adambulacral spines intermixed with stalked clustered pedicellariae (Fig. 4).

Possible Misidentifications

Among the large five-armed sea stars, *Pisaster* species are noted for their thick arms, low papillate dorsal spines and

pedicellariae. Two other Asteroiidae species share these characteristics: (1) *Evasterias troschellii* is a low intertidal species with a small disc and slender arms compared to *P. ochraceus* and a varied, though generally orange-red coloration (Mah 2007). *Evasterias troschellii* has clusters of pedicellariae on its adambulacral spines, not just at their bases as in *P. ochraceus*. (2) *Orthasterias koehleri* has sharp dorsal spines, not blunt papillate ones. These spines are each surrounded by a distinct ring of large pedicellariae and the dorsal spines are arranged in distinct radial rows (those of *P. ochraceus* are not). *Orthasterias koehleri* is often red with yellow mottling and it occurs in the low intertidal and subtidally (Mah 2007).

Two other species of *Pisaster* can be found locally: (1) *Pisaster brevispinus* occurs not on rocks and pilings but on soft substrates, where it feeds on clams. Its aboral spines do not form reticulated patterns or arcs, but occur singly or in groups of two or three, and are separated by areas of soft tissue. *Pisaster brevispinus* has a straight, distinct row of mid-dorsal spines on each arm. This sea star is nearly always pink and it can be mottled with gray-green or maroon-purple color as well (Mah 2007). It is one of the largest asteroiids, growing to 320 mm in diameter (Hyman 1955). (2) *Pisaster giganteus* is bluish gray and its dorsal spines are blunt, clubbed, each surrounded by a ring of blue flesh and around that a ring of pedicellariae. It has tiny pedicellariae that are thickly scattered between the dense spines and its spines are not arranged in radial or concentric rows. *Pisaster giganteus* is a low intertidal sea star usually found further south than Oregon. Despite its name, it is usually smaller than *P. ochraceus* (Ricketts and Calvin 1971; Mah 2007).

Sea stars are extremely variable intra-specifically. Fisher listed three forms ("forma") of *P. ochraceus* (Fisher 1930). Although these names are not used, taxonomically, it should be noted that the Puget Sound, Washington and Oregon outer coast variety of *P. ochraceus* has a flatter, smoother surface ornamentation than does our Oregon bay form (Roberts, personal communication). Subspecies have also been reported for *P. ochraceus*

including *P. o. ochraceus* (north of Point Conception, California) and *P. o. segnis* (south of Point Conception) (Clark 1996), but morphological evidence and genetic homogeneity across populations of supposed subspecies and morphological forms (e.g. “forma” Fisher 1930; Harley et al. 2006) supports the single species *P. ochraceus* (Stickle et al. 1992; Lambert 2000; Frontana-Uribe et al. 2008; see also <http://echinoblog.blogspot.com/search/label/Pisaster%20ochraceus>).

Ecological Information

Range: Type locality is near Willapa Bay, Washington (Ahearn 1995). Range includes Sitka, Alaska south to Baja, Mexico (Ricketts and Calvin 1971). Reported subspecies with differing distribution include *P. o. ochraceus*, occurring north of Point Conception, California and *P. o. segnis*, which is found south of Point Conception (Clark 1996). However, these populations are likely a single species based on morphological and molecular evidence (e.g. Frontana-Uribe et al. 2008).

Local Distribution: Locally in Coos Bay and along the rocky shores of Cape Arago. Typically occurs on the open sea coast as well as in bays on jetties and pilings only in marine parts of large bays.

Habitat: Jetties, rocks, pilings, bay mussel beds and hard substrates. Larger individuals can stand prolonged exposure to air (Feder 1970). Body morphology has been shown to correlate with wave exposure, where thinner and lighter individuals are found in areas with more intense wave exposure (Hayne and Palmer 2013).

Salinity: Collected at salinities of 30 or higher and cannot tolerate long-term exposure to reduced salinities.

Temperature: Cold to temperate. *Pisaster ochraceus* is more tolerant to aerial exposure than other *Pisaster* species, e.g. *P. brevispinus*, (up to 50 hours exposure), but does not tolerate warm temperatures and/or low oxygen levels (Feder 1980).

Tidal Level: Intertidal to 88 meters (Feder 1980). Large sea stars usually found at low tide mark in Puget Sound, Washington (probably for warmth), but they do not move to the lower intertidal in Monterey, California (Feder 1970).

Associates: Mussels, barnacles, limpets and other snails. Other inhabitants of the mussel bed include polychaetes, anemones and nematodes. On pilings in quiet waters, associates include barnacles, anemones (e.g. *Metridium senile*) and tunicates (Ricketts and Calvin 1971). The parasitic ciliate *Orchitophrya stellarum* causes castration in males (Leighton et al. 1991). Several incidences of sudden sea star die off have occurred since 1972, but the most recent to the northwest coast of North America began in June 2013 and is called sea star wasting disease. Affected individuals have ectodermal lesions and tissue decay that eventually leads to death (within 2–3 days). The water-vascular system loses the ability to maintain hydrostatic pressure and individuals often look flaccid when infected. Increased temperature further heightens infection intensity (Bates et al. 2009). The current die off of sea stars is the most significant due to its widespread geographic range and large number of species infected (Hewson et al. 2014). Recently, researchers determined this disease is most likely associated with a family of single stranded DNA viruses (densovirus, *Parvoviridae*) and is now called sea star-associated densovirus (SSaDV). Incidentally, this same virus was detected in museum specimens and, thus, may have been present on the Pacific coast and undetected since those specimens were collected in 1942. Although the specific pathogen is not known in certainty, SSaDV is currently the most likely candidate (Hewson et al. 2014).

Abundance: The most conspicuous sea star of rocky intertidal areas (Puget Sound, Washington, Kozloff 1993; Mah 2007).

Life-History Information

Reproduction: Forcipulate asteroids primarily have separate sexes and free-swimming planktonic larvae (Fisher 1930; Chia et al. 1987). *Pisaster* species do not brood their eggs or young as do some Asteriidae (e.g. *Leptastarias*, Mah 2007). Many species can be induced to spawn and are routinely used in developmental research. One pair of gonads is present in each arm and, when spawning, sea stars lift their body supported by their arms and gametes are released through gonopores on the aboral surface (Chia et al. 1987). Ten gonads, like feathery tufts, two in each ray, occur next to

the central disc in *P. ochraceus*. The spawning period is from March to June (Monterey, California Feder 1956, 1980) with peak spawning from May–June (San Juan Islands, Washington, Chia et al. 1987; Miller 2001). Eggs of *P. ochraceus* are pale orange and 150–160 µm in diameter and a 400 g female can produce up to 40 million eggs (Menge 1975). The gametogenic cycle of both sexes is regulated by photoperiod (Chia et al. 1987). At 12°C, development proceeds as follows: 2 cells at 5hr, 4 cells at 6hr, 8 cells at 7hr, hatching at 29–32 hr, gastrula at 44–63 hr, planktotrophic bipinnaria larva at 5d post fertilization (Chia et al. 1987).

Larva: Embryos develop into planktotrophic larvae called bipinnariae (Chia et al. 1987; Miller 2001). These larvae are approximately 400 µm in length and metamorphose into juvenile sea stars after 76–228 days when they are 0.5 mm in length. Bipinnaria larvae are easily recognizable in the plankton (Fig. 26.1, 26.2, Chia et al. 1987), they are large, fleshy and uniformly ciliated with a distinct, continuous ciliated band that is used for feeding and swimming. Larvae have a large mouth, esophagus, intestine and anus. They can have many long arms, increasing in number with age and can become long and floppy (Fig. 3, Miller 2001). The juvenile sea star develops from the left posterior portion of the larval body. Late stage bipinnaria develop three arms (called brachiolar arms) and a central adhesive disc, anteriorly. Larvae at this stage are called brachiolaria (see Fig. 4, Miller 2001) and they use these arms to attach to the substratum at metamorphosis.

Juvenile: Sexual maturity is reached at five years when individuals are 70–95 g (wet weight) (Menge 1975).

Longevity:

Growth Rate: Varies with food availability and microhabitat (e.g. wave exposure). With constant food supply and proper conditions, a sea star can feed continuously and increase its weight from 2–30 times in a year (Feder 1970). It can survive at least 20 months without feeding. An individual's size is not related as much to age as to food availability. Calmer conditions in a bay ensure greater opportunities for feeding than do open coast conditions (Feder 1970). Asexual regeneration of arms is a characteristic of the Asteroidea. Regeneration of entire individual can occur from small portions of the arm, but

is not possible without some portion of the central disc (Fisher 1930).

Food: Omnivorous (Mauzey et al. 1968). Favorite prey seems to include *Mytilus* (Mauzey et al. 1968), on which it grows fastest, but individuals also eat barnacles, clams, crabs, chitons. Prey items (e.g. mussels) are pulled open such that *P. ochraceus* can insert its stomach and begin digesting material externally. Individuals may feed year-round in central California, but less in winter months in Puget Sound, Washington (Feder 1980). Somewhat aggressive predators, *Pisaster* species are known to elicit escape responses in a variety of prey items (e.g. mollusks, crabs, other sea stars, Feder 1980). The common predator of the lower *Mytilus* beds (Ricketts and Calvin 1971). In the 1969, Paine described the selective predation of *P. ochraceus* on *Mytilus* species in shaping community structure and coined the term “keystone species” for *P. ochraceus*. Predation by *P. ochraceus* shapes the vertical zonation and community structure of rocky intertidal communities (e.g. Paine 1974, 1976, 1995; Mah and Blake 2012).

Predators: Seagulls (on adults), and other sea stars (e.g. *Solaster dawsoni*, Van Veldhuizen and Oakes 1981).

Behavior: Can right itself vigorously when oral surface is detached from substrate and can modulate store of fluid in response to outside air temperature during low tide (Pincebourde et al. 2009). Some invertebrates, (e.g. limpet *Lottia*) can avoid *P. ochraceus* by a special escape mechanism (see *Lottia pelta* in this guide).

Bibliography

1. AHEARN, C. G. 1995. Catalog of the type specimens of seastars (Echinodermata: Asteroidea) in the National Museum of Natural History, Smithsonian Institution. Smithsonian Contributions to Zoology. 572:1-59.
2. BATES, A. E., B. J. HILTON, AND C. D. G. HARLEY. 2009. Effects of temperature, season and locality on wasting disease in the keystone predatory sea star *Pisaster ochraceus*. Diseases of Aquatic Organisms. 86:245-251.

3. BOOLOOTIAN, R. A. 1966. Physiology of Echinodermata. Wiley Interscience, New York.
4. CLARK, A. M. 1996. An Index of names of recent Asteroidea: Part 3. Velatida and Spinulosida, p. 183-250. *In: Echinoderm studies*. Vol. 5. M. Jangoux and J. M. Lawrence (eds.). A. Balkema International Publishers, Rotterdam, Netherlands.
5. DYAKONOV, A. M. 1950. Sea star (Asteroidea) of the U.S.S.R. Seas. Israel Program for Scientific Translations, Smithsonian-NSF, Washington, D.C.
6. FEDER, H. M. 1956. Natural history studies on the starfish *Pisaster ochraceus* (Brandt, 1835) in the Monterey Bay Area. Ph.D. Stanford University, Stanford, CA.
7. FEDER, H. M. 1970. Growth and predation by the ochre sea star *Pisaster ochraceus* in Monterey Bay, California. *Ophelia*. 8:161-185.
8. FEDER, H. M. 1980. Asteroidea: the sea stars, p. 117-135. *In: Intertidal invertebrates of California*. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, CA.
9. FISHER, W. K. 1930. Asteroidea of the north Pacific and adjacent Waters. Government Printing Office, Washington, DC.
10. FRONTANA-URIBE, S., J. DE LA ROSA-VELEZ, L. ENRIQUEZ-PAREDES, L. B. LADAH, AND L. SANVICENTE-ANORVE. 2008. Lack of genetic evidence for the subspeciation of *Pisaster ochraceus* (Echinodermata: Asteroidea) in the north-eastern Pacific Ocean. *Journal of the Marine Biological Association of the United Kingdom*. 88:395-400.
11. HARLEY, C. D. G., M. S. PANKEY, J. P. WARES, R. K. GROSBERG, AND M. J. WONHAM. 2006. Color polymorphism and genetic structure in the sea star *Pisaster ochraceus*. *Biological Bulletin*. 211:248-262.
12. HAYNE, K. J. R., AND R. A. PALMER. 2013. Intertidal sea stars (*Pisaster ochraceus*) alter body shape in response to wave action. *Journal of Experimental Biology*. 216:1717-1725.
13. HEWSON, I., J. B. BUTTON, B. M. GUDENKAUF, B. MINER, A. L. NEWTON, J. K. GAYDOS, J. WYNNE, C. L. GROVES, G. HENDLER, M. MURRAY, S. FRADKIN, M. BREITBART, E. FAHSBENDER, K. D. LAFFERTY, M. A. KILPATRICK, M. C. MINER, P. RAIMONDI, L. LAHNER, C. S. FRIEDMAN, S. DANIELS, M. HAULENA, J. MARLIAVE, C. A. BURGE, M. E. EISENLORD, AND D. C. HARVELL. 2014. Densovirus associated with sea-star wasting disease and mass mortality. *Proceedings of the National Academy of Sciences of the United States of America*. 111:17278-17283.
14. HYMAN, L. H. 1955. *The Invertebrates: Echinodermata*. McGraw-Hill, New York.
15. KOZLOFF, E. N. 1993. *Seashore life of the northern Pacific coast: an illustrated guide to northern California, Oregon, Washington, and British Columbia*. University of Washington Press, Seattle, WA.
16. LAMBERT, P. 2000. *Sea stars of British Columbia, Southeast Alaska and Puget Sound*. UBC Press, Vancouver, B.C.
17. LEIGHTON, B. J., J. D. G. BOOM, C. BOULAND, E. B. HARTWICK, AND M. J. SMITH. 1991. Castration and mortality in *Pisaster ochraceus* parasitized by *Orchitophyra stellarum* (Ciliophora). *Diseases of Aquatic Organisms*. 10:71-73.
18. MAH, C. 2007. Echinodermata: Asteroidea, p. 922-930. *In: The Light and Smith manual: intertidal invertebrates from central California to Oregon*. J. T. Carlton (ed.). University of California Press, Berkeley, CA.
19. MAH, C. L., AND D. B. BLAKE. 2012. Global diversity and phylogeny of the Asteroidea (Echinodermata). *Plos One*. 7:DOI: 10.1371/journal.pone.0035644.
20. MAUZEY, K. P., A. C. BIRKELAND, AND P. K. DAYTON. 1968. Feeding behavior of asteroids and escape responses of the prey in the Puget Sound region. *Ecology*. 49:603-619.
21. MENGE, B. A. 1975. Brood or broadcast? Adaptive significance of

- different reproductive strategies in two intertidal seastars *Leptasterias hexactus* and *Pisaster ochraceus*. *Marine Biology*. 31:87-100.
22. MILLER, B. A. 2001. Echinodermata, p. 270-290. *In: An Identification guide to the larval marine invertebrates of the Pacific Northwest*. A. L. Shanks (ed.). Oregon State University Press, Corvallis, OR.
 23. PAINE, R. T. 1974. Intertidal community structure: experimental studies on relationship between a dominant competitor and its principal predator. *Oecologia*. 15:93-120.
 24. PAINE, R. T. 1976. Size limited predation: observational and experimental approach with *Mytilus-Pisaster* interaction. *Ecology*. 57:858-873.
 25. PAINE, R. T. 1995. A conversation on refining the concept of keystone species. *Conservation Biology*. 9:962-964.
 26. PINCEBOURDE, S., E. SANFORD, AND B. HELMUTH. 2009. An intertidal sea star adjusts thermal inertia to avoid extreme body temperatures. *American Naturalist*. 174:890-897.
 27. STICKLE, W. B., D. W. FOLTZ, M. KATOH, AND H. L. NGUYEN. 1992. Genetic structure and mode of reproduction in five species of sea stars (Echinodermata: Asteroidea) from the Alaskan coast. *Canadian Journal of Zoology*. 70:1723-1728.
 28. VANVELDHUIZEN, H. D., AND V. J. OAKES. 1981. Behavioral responses of seven species of asteroids to the asteroid predator, *Solaster dawsoni*. *Oecologia*. 48:214-220.
 29. WOBBER, D. R. 1975. Agonism in asteroids. *Biological Bulletin*. 148:483-496.

Updated 2015

T.C. Hiebert and L. Hiebert

Chordata

Botrylloides violaceus

A colonial ascidian, or tunicate

Phylum: Chordata
Class: Ascidiacea
Order: Stolidobranchia
Family: Styelidae

Description

Size—colonies can be several cm across (Abbott and Newberry 1980, Saito et al. 1981); individual zooids 1-2 mm long (as seen from above); diameter about ½ length (fig. 1). Zooids arranged in rows or "systems": often ladderlike (unless crowded), with a common cloacal cavity between rows (fig. 1). Often with many dozen individuals in flat, encrusting colony.

Color—variable; these specimens (Coos Bay) light yellow-orange, or tan; can be gray, orange: possibly light dependent (Berrill 1947). "Test" (see below) clear.

Zooids—oblong, more or less free (Lambert 2003); each with raised oral aperture; cloaca is shared with zooids across "ladder". With one large ovary on each side of body: genus *Botrylloides* (Van Name 1945). Asexual buds develop on zooid walls or from ampullae (vascular buds) at colony edges (figs. 1a, 3). Incubating pouches develop from ovaries: genus *Botrylloides* (Abbott and Newberry 1980).

Tunic or Test—an external connective tissue; transparent in these specimens.

Mantle—the true body wall: a thin, sac-like membrane inside test, containing muscle and blood vessels, and enclosing the internal parts (Van Name 1945) (fig. 3a).

Ampullae—enlarged, blind, blood reservoirs around edges of tunic; finger-shaped. Can give rise to new zooids by vascular budding. Ampullae also have a respiratory function.

Oral Aperture—on anterior surface; round, smooth-edged, raised, with small simple tentacles inside; four-lobed siphon (fig. 1).

Tentacles—simple; 4 large (these specimens), several small ones (fig. 1).

Cloaca—common, between rows of zooids (figs. 1a, 2a). Atrial apertures of zooids (fig. 3) are below surface of colony (fig. 3a).

Pharynx—(branchial sac or pharyngeal basket); posteriorly it leads to esophagus, stomach, and intestine. This structure contains stigmata (stills) and cilia for filtering food. It has 3 inner long vessels or bars, but no longitudinal folds separating stigmata (Berrill 1947) (fig. 3a). Species lacks an

abdomen: body not divided as in some elongate solitary ascidians (fig. 3).

Endostyle—a deep groove on ventral side of pharynx (side opposite atrial siphon); contains long glandular bands (Berrill 1947), which produce mucus used for feeding (fig. 3a).

Dorsal Lamina—a membranous ridge, projecting inward from the dorsal midline of the pharynx (atrial siphon side) (fig. 3a). Dorsal lamina rolls mucus sheets into a cord, after receiving them from endostyle across sac walls (Goodbody 1974).

Stigmata—slits in pharynx walls, in groups between longitudinal vessels (figs. 1, 3, 3a).

Atrium—cavity surrounding pharynx. Water enters atrium via stigmata, and exits by atrial siphon (fig. 3a).

Gonads—genus characterized by a large ovary on each side of zooid (fig. 3a). Embryo develops in brood pouch in ovum. Testes mulberry-like, anterior to ovum (fig. 3a). (Not visible in zooid in fig. 3.)

Digestive Tract—to left of branchial sac, with narrow loop at base (Berrill 1947) (figs. 3, 3a.)

Larva—Large (up to 3mm in length) "tadpole" type, with long posterior tail containing notochord and slender neural tube. Body contains photolith, a balance and light organ near eye, and several ampullae (fig. 4a) (Saito et al. 1981, Lambert 2003).

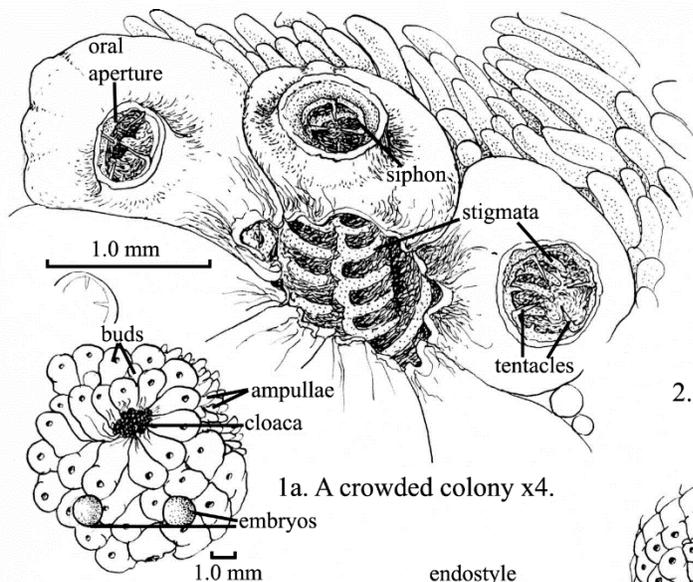
Possible Misidentifications

The family Styelidae contains both solitary and compound forms. Family characteristics include square or 4-lobed apertures, simple filiform tentacles, a continuous dorsal lamina (fig. 3a), and straight longitudinal stigmata. Some genera have 4 curved longitudinal folds in the pharynx, but *Botrylloides* and the closely related *Botryllus* and *Metandrocarpa* do not (Van Name 1945). 4 other genera also lack these longitudinal folds, but do not occur in our area: *Symplegma*, *Kukenthalia*, *Polyzoa* and *Alloeocarpa* (Van Name 1945).

Of the 3 local encrusting colonial Styelidae, *Metandrocarpa* (*dura*) is usually reddish, with large zooids (5-6 mm). It is

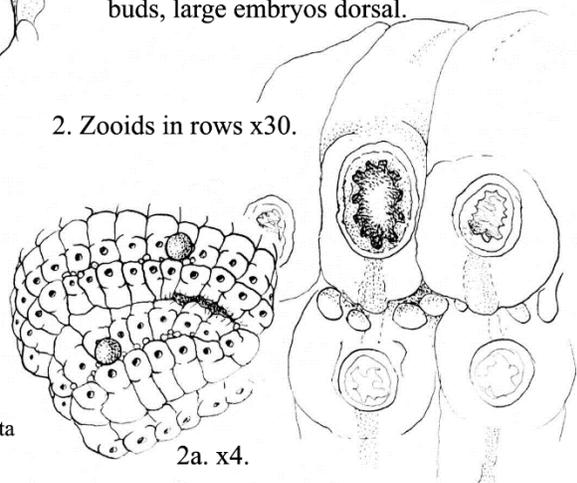
Botrylloides violaceus

1. *Botrylloides violaceus* (L: 1.7mm, W: 1.0mm) x30:
zooids; round oral aperture with four-lobed siphon, simple tentacles; common cloacal cavity; zooid systems in rows or crowded; many dozen zooids possible; ampullae at margins or between rows; buds, large embryos dorsal.



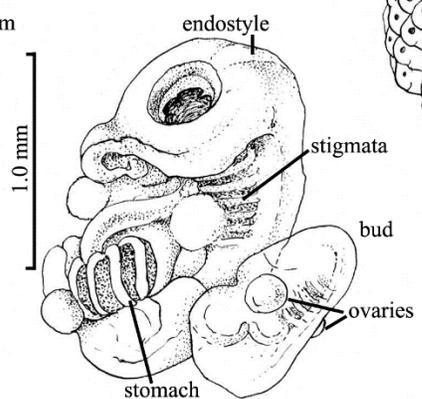
1a. A crowded colony x4.

2. Zooids in rows x30.



2a. x4.

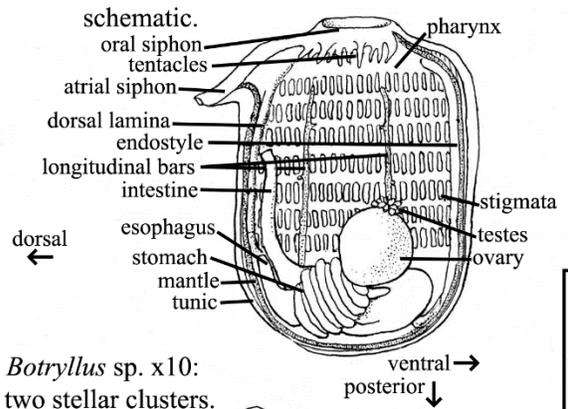
3. Zooid and bud lateral view x40.



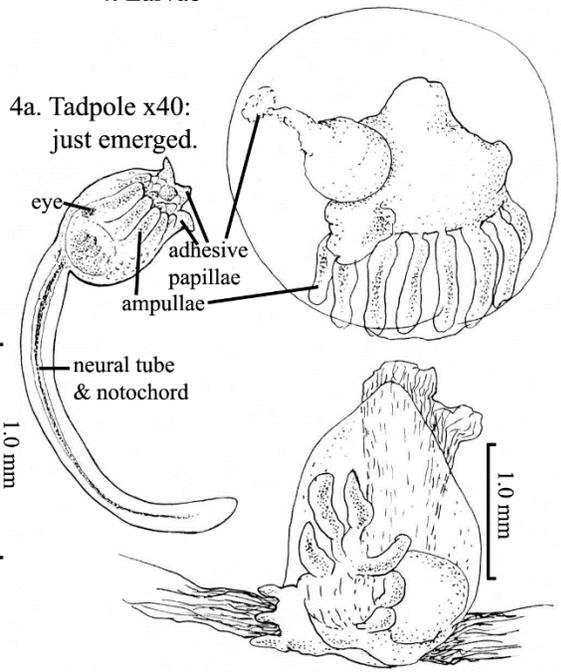
4b. Oozoid x50: about to settle.

4. Larvae

3a. Zooid, schematic.

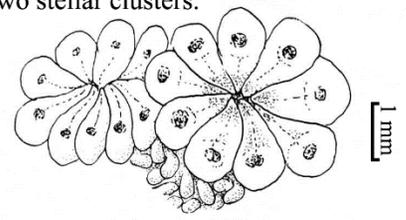


4a. Tadpole x40: just emerged.



4c. Oozoid, settling x25.

5. *Botryllus* sp. x10: two stellar clusters.



not arranged in systems: each zooid has a separate atrial siphon. Zooids are more separate and distinct, being embedded in the tunic, but actually connected only basally. Zooids can seem to be in rows and laterally fused, however.

Botryllus spp., a cosmopolitan genus, is often found with *Botrylloides* on floats, and is difficult to distinguish from it. *Botryllus* always forms circular or star-shaped clusters or systems; it never has more than 20 zooids in a system. (*Botrylloides* forms systems composed of long double rows or clumps of zooids, and often has several dozen zooids in a system.) Because of the shape of the colony, *Botryllus* zooids tend to be tear-shaped, with a “languet” or tongue-shaped atrial end (Van Name 1945) (fig. 5); *Botrylloides* zooids are usually oval-shaped. *Botryllus* individuals lack the brood pouch of *Botrylloides*; their young develop in the atrium before being extruded. A further difference between the 2 species is that *Botryllus* has the ovaries anterior to the testes (the reverse of *Botrylloides*), and can have 1 or several ovaries; *Botrylloides* has 1 large ovary on each side.

There have been several named species of *Botrylloides*, but the species from our area have not yet been studied. Van Name 1945 discusses *Botrylloides magnum* from Alaska, but it is very large, and poorly described. *B. diegensis* is a southern California form, with brown and purple zooids and test vessels. The European *B. leachi* and the Japanese *B. violaceus* have not been identified from our coast.

Ecological Information

Range—genus worldwide

Local Distribution—Coos Bay: Charleston small boat harbor.

Habitat—on floating docks, (Coos Bay); in bays and harbors (Abbott and Newberry 1980). Ascidians represent a significant percentage of the fouling organism community (Miller 1971, Simkanin et al. 2012).

Salinity—collected at 30 ‰ (Coos Bay).

Temperature—10-15 °C (Coos Bay).

Tidal Level—low intertidal and shallow subtidal (Abbott and Newberry 1980).

Associates—*Obelia*, caprellid amphipods, *Corophium* amphipods, nereid polychaetes, *Eudistylia*. Ascidians are commensal

hosts to notodelphid copepods, amphipods, and host to some specific parasitic copepods (Miller 1971).

Quantitative Information

Weight—

Abundance—locally common on floating docks, especially in summer.

Life History Information

Reproduction—hermaphroditic, ovoviviparous. Asexual budding also occurs. Sexual fertilization internal; embryos develop in ovary (1 to a zooid), emerge as tadpoles (Saito et al. 1981, Zaniolo et al. 1998). Larvae develop quickly, settle soon (in only a few minutes) and metamorphose to form new zooids (fig. 4). Sexual reproduction in late spring, early summer. Larvae release determined by light. Buds can develop from parent (fig. 3), or from bases of vascular ampullae at colony's edge. (Numerous buds of all types abort during development.)

Growth Rate—colonies of *Botryllus* sp. reach maturity in 1-2 months' time (MacGinitie 1939).

Longevity—an ascidian colony may live more than 3 years; an individual zooid less than a year (Berrill 1947).

Food—ciliary mucus feeders, filtering plankton through the tentacles.

Predators—ascidians: probably fish, crab, polychaetes, sea stars; especially prosobranch molluscs, opisthobranchs, nudibranchs, turbellarian flatworms. Also grey seal (Scotland); man, for food, Japan. Mediterranean, Chile; bait, Australia, S. Africa. Destroyed as a pest in oyster beds, commercial fishing grounds (Miller 1971).

Behavior—zooids are sessile; tadpole larvae can swim, but tend to settle near parents, attaching with adhesive papillae.

Bibliography

1. ABBOTT, D. P. and A. T. NEWBERRY. 1980. Chapter 12: Urochordata: The Tunicates, p. 177-226. *In*: Intertidal invertebrates of California. R. H. Morris, D. P. Abbott, and E. C. Haderlie (eds.). Stanford University Press, Stanford, California, Stanford, California.
2. BERRILL, N. J. 1947. The developmental cycle of *Botrylloides*. The Quarterly journal of microscopical science. 88:393-407.

3. GOODBODY, I. 1974. The physiology of ascidians. *Advances in Marine Biology*. 12:1-149.
4. MACGINITIE, G. E. 1939. The Method of feeding of tunicates. *Biological Bulletin*. 77:443-447.
5. MILLER, R. H. 1971. The biology of ascidians. *Advances in Marine Biology*. 9:1-100.
6. VAN NAME, W. G. 1945. The North and South American ascidians. *Bulletin of the American Museum of Natural History*. 841:1-476.
7. Cohen, A.N. and J.T. Carlton. (1995). Nonindigenous Aquatic Species in a United States Estuary: A Case Study of the Biological Invasions of the San Francisco Bay and Delta. U.S. Fish and Wildlife Service, Washington, DC (pp. 111-112).
8. Lambert, G. (2003). New records of ascidians from the NE Pacific: a new species of *Tridemnum*, range extension and description of *Aplidiopsis pannosum* (Ritter, 1899), including its larva, and several non-indigenous species. *Zoosystema* 24: 665-675.
9. Saito, Y., Mukai, H., Watanabe, H. (1981). Studies on Japanese compound styelid ascidians II. A new species of the genus *Botrylloides* and redescription of *B. violaceus* Oka., *Publications of the Seto Marine Biological Laboratory* 26: 357-368
10. Simkanin, C., Davidson, I. C., Dower, J. F., Jamieson, G. Therriault, T. W. (2012). Anthropogenic structures and the infiltration of natural benthos by invasive ascidians. *Marine Ecology* 33: 499-511
11. Zaniolo, G., Manni, L., Brunetti, R., & Burighel, P. (1998). Brood pouch differentiation in *botrylloides violaceus*, a viviparous ascidian (tunicata). *Invertebrate Reproduction & Development*, 33(1), 11-23.

Updated 2014

A. Burgess

Appendix A: Alphabetical list of species by genus

<i>Abarenicola pacifica</i>	90
<i>Adula californiensis</i>	714
<i>Aequorea victoria</i>	2
<i>Alderia modesta</i>	658
<i>Allorchestes angusta</i>	306
<i>Americorophium brevis</i>	282
<i>Americorophium salmonis</i> ...	288
<i>Americorophium spinicorne</i>	294
<i>Amphiporus imparispinosus</i> ...	80
<i>Ampithoe lacertosa</i>	258
<i>Ampithoe valida</i>	264
<i>Anthopleura artemisia</i>	26
<i>Anthopleura elegantissima</i> ...	32
<i>Aplysiopsis enteromorphae</i>	662
<i>Archaeomysis grebnitzkii</i>	538
<i>Armandia brevis</i>	104
<i>Assiminea californica</i>	604
<i>Balanus crenatus</i>	568
<i>Balanus glandula</i>	574
<i>Balanus nubilus</i>	586
<i>Bankia setacea</i>	706
<i>Boccardia proboscidea</i>	208
<i>Botrylloides violaceus</i>	846
<i>Callianax biplicata</i>	632
<i>Cancer antennarius</i>	366
<i>Cancer magister</i>	372
<i>Cancer oregonensis</i>	380
<i>Cancer productus</i>	386
<i>Capitella spp.</i>	94
<i>Caprella drepanochir</i>	328
<i>Carinoma mutabilis</i>	56
<i>Cerebratulus californiensis</i>	68
<i>Cerebratulus marginatus</i>	72
<i>Chlorostoma funebris</i>	596
<i>Clinocardium nuttallii</i>	738
<i>Corbicula fluminea</i>	746
<i>Crangon alaskensis</i>	434
<i>Crangon franciscorum</i>	440
<i>Cryptomya californica</i>	674
<i>Cumella vulgaris</i>	476
<i>Detonella papillicornis</i>	490
<i>Diadumene lineata</i>	38
<i>Ectopleura crocea</i>	20
<i>Entodesma navicula</i>	732
<i>Eobrolgus spinosus</i>	310
<i>Eogammarus confervicolus</i> ..	270
<i>Eohaustorius estuarius</i>	300
<i>Eteone lighti</i>	176
<i>Eteone pacifica</i>	182
<i>Eudistylia vancouveri</i>	196

<i>Glycera robusta</i>	132
<i>Glycinde armigera</i>	138
<i>Gnorimosphaeroma insulare</i>	532
<i>Grandidierella japonica</i>	276
<i>Halosydna brevisetosa</i>	188
<i>Hemigrapsus nudus</i>	422
<i>Hemigrapsus oregonensis</i> ...	428
<i>Heptacarpus paludicola</i>	452
<i>Heptacarpus sitchensis</i>	458
<i>Hermisenda crassicornis</i> ...	644
<i>Hesperonoe complanata</i>	192
<i>Hiatella arctica</i>	666
<i>Hobsonia florida</i>	236
<i>Ianiropsis derjugini</i>	512
<i>Idotea resecata</i>	504
<i>Idotea wosnesenskii</i>	510
<i>Juga plicifera</i>	628
<i>Lacuna porrecta</i>	608
<i>Lamprops quadriplicata</i>	464
<i>Leitoscoloplos pugettensis</i> ...	116
<i>Leptochelia</i> spp.....	554
<i>Leukoma staminea</i>	802
<i>Ligia pallasii</i>	518
<i>Limnoria tripunctata</i>	526
<i>Lissocrangon stylirostris</i>	446
<i>Lithoglyphus virens</i>	600
<i>Littorina plena</i>	612
<i>Littorina scutulata</i>	618
<i>Littorina sitkana</i>	624
<i>Lottia digitalis</i>	588
<i>Lottia pelta</i>	592
<i>Macoma balthica</i>	778
<i>Macoma inquinata</i>	788
<i>Macoma nasuta</i>	794
<i>Magelona sacculata</i>	202
<i>Mediomastis californiensis</i> ...	100
<i>Megalorchestia pugettensis</i>	316
<i>Mesidotea entomon</i>	482
<i>Metridium senile</i>	50
<i>Mya arenaria</i>	680
<i>Myosotella myosotis</i>	654
<i>Mytilus trossulus</i>	720
<i>Neanthes brandti</i>	158
<i>Neanthes limnicola</i>	164
<i>Nematostella vectensis</i>	44
<i>Neomysis mercedis</i>	546
<i>Neotrypaea californiensis</i>	336
<i>Nephtys caeca</i>	146
<i>Nephtys caecoides</i>	152
<i>Nereis vexillosa</i>	170
<i>Nippoleucon hinumensis</i>	470

<i>Nucella lamellose</i>	636
<i>Nucella ostrina</i>	640
<i>Nutricola tantilla</i>	812
<i>Obelia longissimi</i>	8
<i>Onchidoris bilamellata</i>	650
<i>Ophelia assimilis</i>	108
<i>Owenia collaris</i>	126
<i>Pachygrapsus crassipes</i>	398
<i>Pagurus hirsutiusculus</i>	366
<i>Paranemertes peregrina</i>	84
<i>Paraonaella platybranchia</i>	122
<i>Penitella penita</i>	690
<i>Petrolisthes cinctipes</i>	352
<i>Phascolosoma agassizi</i>	252
<i>Phoronis pallida</i>	828
<i>Pinnixa faba</i>	410
<i>Pisaster brevispinus</i>	832
<i>Pisaster ochraceus</i>	838
<i>Pista pacifica</i>	242
<i>Polydora nuchalis</i>	214
<i>Polyorchis penicillatus</i>	14
<i>Pseudopolydora kemp</i>	218
<i>Pugettia producta</i>	392
<i>Pygospio elegans</i>	224
<i>Ramphogordius sanguineus</i> ..	76
<i>Rhithropanopeus harrisi</i>	404
<i>Saxidomus giganteus</i>	820
<i>Scleroplax granulata</i>	416
<i>Scolelepis foliosa</i>	230
<i>Scoletoma zonata</i>	142
<i>Semibalanus cariosus</i>	560
<i>Siliqua patula</i>	764
<i>Solen sicarius</i>	772
<i>Thelepus crispus</i>	246
<i>Thoracophelia mucronata</i>	112
<i>Traskorchestia traskiana</i>	322
<i>Tresus capax</i>	756
<i>Tubulanus polymorphus</i>	60
<i>Tubulanus sexlineatus</i>	64
<i>Upogebia pugettensis</i>	358
<i>Zirfaea pilsbryi</i>	698

Appendix B: Common and previous names used in this work

Acorn barnacle.....	see	<i>Balanus glandula</i>
<i>Aequorea aequorea</i>	see	<i>Aequorea victoria</i>
Aggregating anemone.....	see	<i>Anthopleura elegantissima</i>
Alaskan bay shrimp.....	see	<i>Crangon alaskensis</i>
<i>Aplysiopsis smithi</i>	see	<i>Aplysiopsis enteromorphae</i>
Arctic saxicave.....	see	<i>Hiatella arctica</i>
Asian clam, the.....	see	<i>Corbicula fluminea</i>
Basket cockle.....	see	<i>Clinocardium nuttallii</i>
Bay mussel, the.....	see	<i>Mytilus trossulus</i>
Beefsteak clam.....	see	<i>Saxidomus giganteus</i>
Bent-nosed clam, the	see	<i>Macoma nasuta</i>
Fine-checkedered periwinkle.....	see	<i>Littorina plena</i>
Black turban snail, the.....	see	<i>Chlorostoma funebris</i>
Blue mud shrimp, the.....	see	<i>Upogebia pugettensis</i>
Blunt jackknife clam.....	see	<i>Solen sicarius</i>
Buried anemone.....	see	<i>Anthopleura artemisia</i>
Butter clam.....	see	<i>Saxidomus giganteus</i>
<i>Callianassa californiensis</i>	see	<i>Neotrypaea californiensis</i>
<i>Capitella capitata</i>	see	<i>Capitella</i> sp.
Checkedered periwinkle.....	see	<i>Littorina scutulata</i>
Clonal anemone.....	see	<i>Anthopleura elegantissima</i>
<i>Collisella digitalis</i>	see	<i>Lottia digitalis</i>
<i>Collisella pelta</i>	see	<i>Lottia pelta</i>
Common gray shrimp.....	see	<i>Crangon franciscorum</i>
Common Pacific sea star.....	see	<i>Pisaster ochraceus</i>
Common shrimp.....	see	<i>Lissocrangon stylirostris</i>
<i>Corophium brevis</i>	see	<i>Americorophium brevis</i>
<i>Corophium salmonis</i>	see	<i>Americorophium salmonis</i>
<i>Corophium spinicorne</i>	see	<i>Americorophium spinicorne</i>
Crenulated barnacle, the.....	see	<i>Balanus crenatus</i>
Crystal jelly.....	see	<i>Aequorea victoria</i>
Dungeness crab.....	see	<i>Cancer magister</i>
<i>Entodesma saxicola</i>	see	<i>Entodesma navicula</i>
<i>Euzonus mucronata</i>	see	<i>Thoracophelia mucronata</i>
False <i>Mya</i>	see	<i>Cryptomya californica</i>
Fat gaper.....	see	<i>Tresus capax</i>
Feathery shipworm.....	see	<i>Bankia setacea</i>
Flat porcelain crab, the.....	see	<i>Petrolisthes cinctipes</i>
Flat razor clam, the.....	see	<i>Siliqua patula</i>
Frilled anemone.....	see	<i>Metridium senile</i>
Frilled dogwinkle, the.....	see	<i>Nucella lamellosa</i>

Gaper clam, the.....	see	<i>Tresus capax</i>
Ghost shrimp, the.....	see	<i>Neotrypaea californiensis</i>
Giant barnacle, the.....	see	<i>Balanus nubilus</i>
Giant Columbia River spire shell.....	see	<i>Lithoglyphus virens</i>
Glass shrimp.....	see	<i>Heptacarpus sitchensis</i>
Graceful keeled horn snail.....	see	<i>Juga plicifera</i>
Hairy hermit crab.....	see	<i>Pagurus hirsutiusculus</i>
<i>Haliplanella luciae</i>	see	<i>Diadumene lineata</i>
Hardshell clam.....	see	<i>Leukoma staminea</i>
Heart cockle.....	see	<i>Clinocardium nuttallii</i>
Helmet limpet, the.....	see	<i>Lottia pelta</i>
<i>Hemileucon comes</i>	see	<i>Nippoleucon hinumensis</i>
<i>Heptacarpus pictus</i>	see	<i>Heptacarpus sitchensis</i>
Horseneck clam.....	see	<i>Tresus capax</i>
<i>Ianiropsis kincaidi derjugini</i>	see	<i>Ianiropsis derjugini</i>
Irus clam.....	see	<i>Macoma inquinata</i>
Large mussel worm, the.....	see	<i>Nereis vexillosa</i>
Large proboscis worm, the.....	see	<i>Glycera robusta</i>
<i>Leptocheilia dubia</i>	see	<i>Leptocheilia sp.</i>
Lined shore crab, the.....	see	<i>Pachygrapsus crassipes</i>
<i>Lineus ruber, Lineus sp.</i>	see	<i>Ramphogordius sanguineus</i>
Little gaper.....	see	<i>Hiatella arctica</i>
Littleneck clam.....	see	<i>Leukoma staminea</i>
Lugworm, the.....	see	<i>Abarenicola pacifica</i>
<i>Lumbrineris zonate</i>	see	<i>Scoletoma zonata</i>
Many-gilled onchidoris nudibranch.....	see	<i>Onchidoris bilamellata</i>
Market crab.....	see	<i>Cancer magister</i>
Moonglow anemone.....	see	<i>Anthopleura artemisia</i>
<i>Mytilus edulis</i>	see	<i>Mytilus trossulus</i>
<i>Nereis brandti</i>	see	<i>Neanthes brandti</i>
<i>Nereis limnicola</i>	see	<i>Neanthes limnicola</i>
Nestling saxicave.....	see	<i>Hiatella arctica</i>
Northwest shipworm, the.....	see	<i>Bankia setacea</i>
<i>Nucella emarginata</i>	see	<i>Nucella ostrina</i>
Ochre sea star.....	see	<i>Pisaster ochraceus</i>
<i>Olivella biplicata</i>	see	<i>Callianax biplicata</i>
Orange-striped anemone.....	see	<i>Diadumene lineata</i>
Oregon Cancer crab, the.....	see	<i>Cancer oregonensis</i>
<i>Ovatella myosotis</i>	see	<i>Myosotella myosotis</i>
<i>Owenia fusiformis</i>	see	<i>Owenia collaris</i>
Pacific littleneck.....	see	<i>Leukoma staminea</i>
Pacific peanut worm.....	see	<i>Phascolosoma agassizi</i>
Pacific rock crab.....	see	<i>Cancer antennarius</i>

Pea pod borer, the.....	see	<i>Adula californiensis</i>
Penicillate jellyfish.....	see	<i>Polyorchis penicillatus</i>
<i>Pinauay crocea</i>	see	<i>Ectopleura crocea</i>
Pink sea star.....	see	<i>Pisaster brevispinus</i>
Plumose anemone.....	see	<i>Metridium senile</i>
<i>Protothaca staminea</i>	see	<i>Leukoma staminea</i>
Purple olive, the.....	see	<i>Callianax biplicata</i>
Purple sea star.....	see	<i>Pisaster ochraceus</i>
Purple shore crab, the.....	see	<i>Hemigrapsus nudus</i>
Red nose.....	see	<i>Hiatella arctica</i>
Red rock crab, the.....	see	<i>Cancer productus</i>
Red-eye jellyfish.....	see	<i>Polyorchis penicillatus</i>
Rock cockle.....	see	<i>Leukoma staminea</i>
Rock-dwelling emarginated dogwinkle, the	see	<i>Nucella ostrina</i>
Rock-dwelling entodesma.....	see	<i>Entodesma navicula</i>
Rough piddock, the.....	see	<i>Zirfaea pilsbryi</i>
<i>Saduria entomon</i>	see	<i>Mesidotea entomon</i>
Salt-and-pepper shrimp.....	see	<i>Crangon alaskensis</i>
Sand worm.....	see	<i>Abarenicola pacifica</i>
Shield limpet, the.....	see	<i>Lottia pelta</i>
Short-spined sea star.....	see	<i>Pisaster brevispinus</i>
Sickle razor clam, the.....	see	<i>Solen sicarius</i>
Sitka littorine, the.....	see	<i>Littorina sitkana</i>
Six-lined ribbon worm.....	see	<i>Tubulanus sexlineatus</i>
Smith's unwashed-looking sacoglossan	see	<i>Aplysiopsis enteromorphae</i>
Soft-shelled clam.....	see	<i>Mya arenaria</i>
Starlet sea anemone.....	see	<i>Nematostella vectensis</i>
<i>Tegula funebris</i>	see	<i>Chlorostoma funebris</i>
Top shell snail.....	see	<i>Chlorostoma funebris</i>
<i>Transennella tantilla</i>	see	<i>Nutricula tantilla</i>
Wanderer, the.....	see	<i>Paranemertes peregrina</i>
Washington clam.....	see	<i>Saxidomus giganteus</i>
Wide chink shell, the.....	see	<i>Lacuna porrecta</i>
Wrinkled dogwinkle, the.....	see	<i>Nucella lamellosa</i>

Appendix C: Local (Coos Bay) collection sites mentioned in this text

