20

Urochordata:Ascidiacea

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Widespread interest in the study of tunicates began after Kowalevsky's publications (1886–1871) describing the chordate nature of the ascidian tadpole larva. Since then, larvae from ten families worldwide of the class Ascidiacea have been described (Cloney, 1982). There are ca 60 species of tunicates from ten families found in the waters of the Pacific Northwest (see Tables 1 and 2).

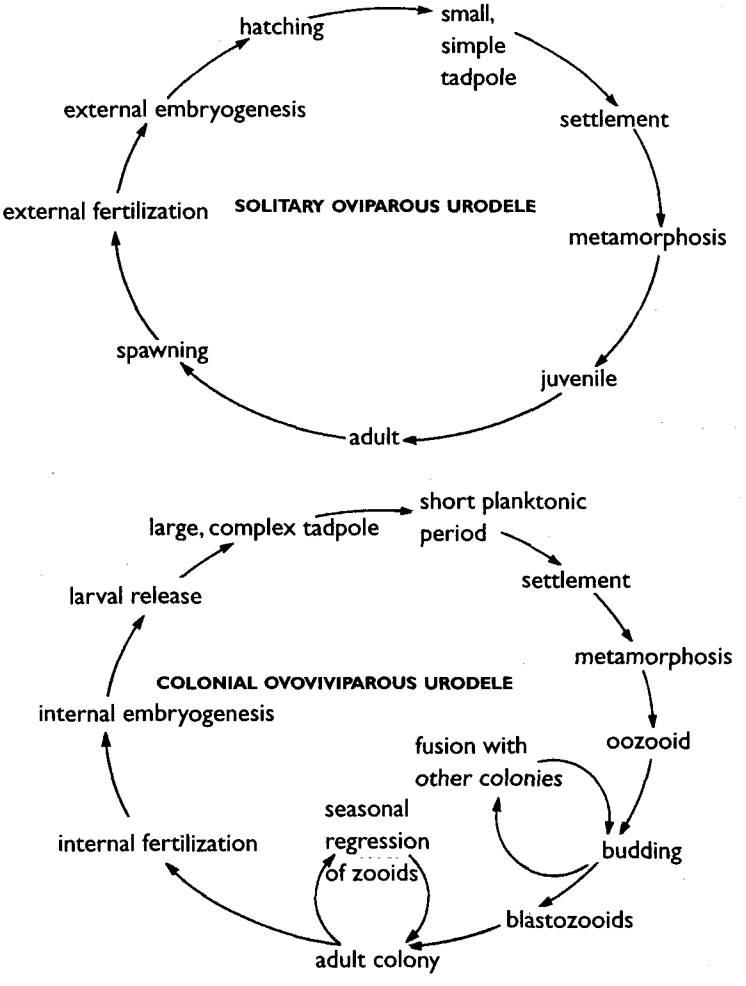

Fig. 1. Generalized life cycles of typical solitary ascidians (top) and compound ascidians (bottom). The diagrams incorporate characteristics of many species, not all aspects of which are present in the life cycle of any given species. (From Svane and Young, 1989)

Reproduction and Development

Ascidian species that reproduce sexually are considered simple ascidians and are solitary. Species that reproduce both sexually and asexually (e.g., through budding) are considered compound ascidians and have a colonial growth form (Berrill, 1975; Strathmann, 1987). Most ascidians are simultaneous hermaphrodites, and examples of both self-fertile species and species that are not self-fertilizing exist (Berrill, 1975). Ascidians may be oviparous (typically solitary forms), ovoviviparous (typically compound forms), or viviparous (Fig. 1). Most solitary oviparous ascidians produce large numbers of relatively small eggs that undergo development into tadpole larvae (Berrill, 1950). Compound ascidians generally produce only a few large eggs that develop into relatively complex tadpole larvae. All ascidian larvae are lecithotrophic, though some are direct-developing and bypass the tadpole stage completely to hatch as small juveniles (e.g., *Molgula pacifica* and *Pelonia corrugata*).

Ascidian tadpole morphology has received considerable study and review (see Millar, 1971; Berrill, 1975; Cloney, 1978, 1982; Katz, 1983; Svane and Young, 1989; Burighel and Cloney, 1997). There is large variation in ascidian size, color, and complexity of internal structures. Compound ascidians have the largest larvae (to 4.5 mm long) and most complex internal anatomy (Fig. 2). Solitary ascidians typically have smaller larvae (to 1.0 mm long) and possess less complex internal anatomy. The surface of all ascidian larvae is covered by a transparent tunic.

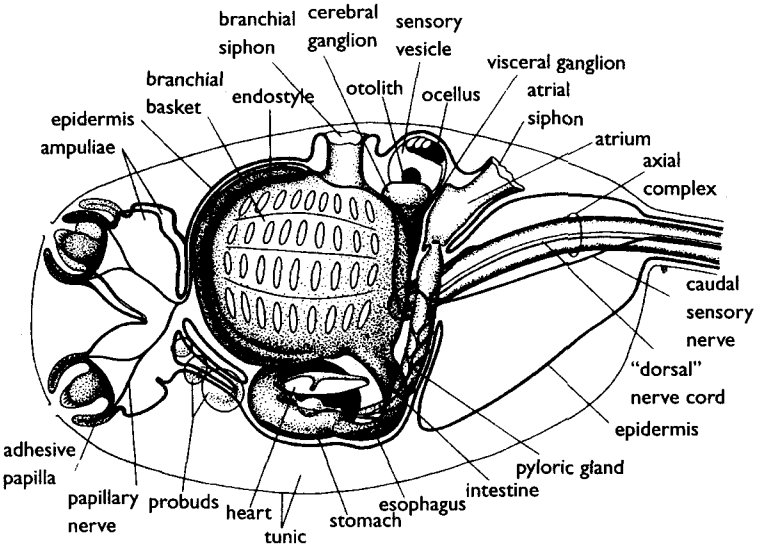

Fig. 2. Diagrammatic compound ascidian larva of *Distalpia occidentalis*. Details of the atrium, inner cuticular layer, and cells of the tunic are omitted. The length of the trunk is 1 mm and of the entire larva, including the caudal fin, 3.2 mm. (From Cloney, 1982)

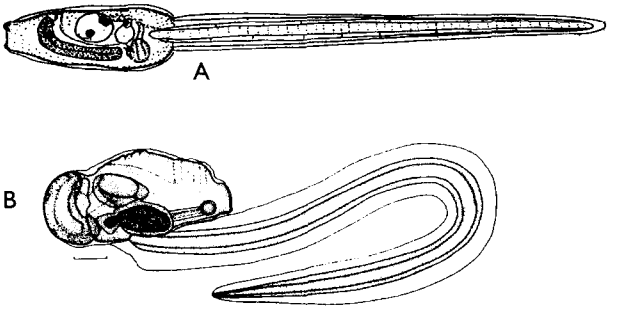

Fig. 3. Basic morphological differences between ascidian tadpole larvae and larvaceans. (A) Ascidian tadpole larva. (B) Larvacean *Oikopleura* sp. Scale = 100 **μm** (A from Berrill, 1947, Fig. 1; B from *A Guide to Marine Coastal Plankton and Marine Invertebrate Larvae*, Second Edition, by DeBoyd L. Smith and Kevin B. Johnson. Copyright 1996 by DeBoyd L. Smith and Kevin B. Johnson. Reprinted by permission of Kendall/Hunt Publishing Company)

Because of the short pelagic duration and small range of dispersal of most tadpole larvae (Svane and Young 1989), the likelihood of encountering them in the plankton is low. Special care should be taken to not confuse them with the more abundant larvaceans, which if superficially examined outside their "houses" are somewhat similar in morphology to tadpole larvae (Fig. 3). The most obvious feature differentiating larvaceans from ascidian tadpole larvae is the position of the tail (S. Bassham, pers. comm.). In ascidian tadpole larvae, the tail protrudes from the posterior end of the trunk; in larvaceans, the tail is shifted to a position about halfway between the mouth and the posterior end of the trunk. Other features present in larvaceans but not tadpole larvae include a mouth at the anterior end of the trunk and gonad masses (in ripe larvaceans).

Identification of Local Taxa

Lacking morphological information on most larval ascidian, this chapter presents a compilation of useful diagnostic characteristics with pictures included when available. From this information identification to species level is not possible for most larvae, though in some cases one may identify the

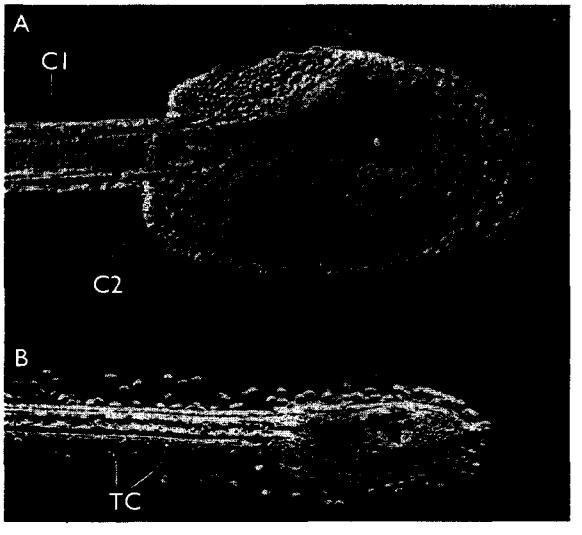

Fig. 4. (A) *Corella inflata*, swimming larval stage, showing the trunk and part of the tail. The outer (C1) and inner (C2) cuticular layers of the tunic are visible. In this species, C2 terminates at the base of the tail. (Total length 0.28 mm.) (B) *Ascidia paratropa*, larval trunk with about half of the tail visible in a lateral view. The outer cuticular layer of tunic (C1) is covered with firmly attached test cells (TC). (Total length 0.54 mm.) (From Burighel and Cloney, 1997)

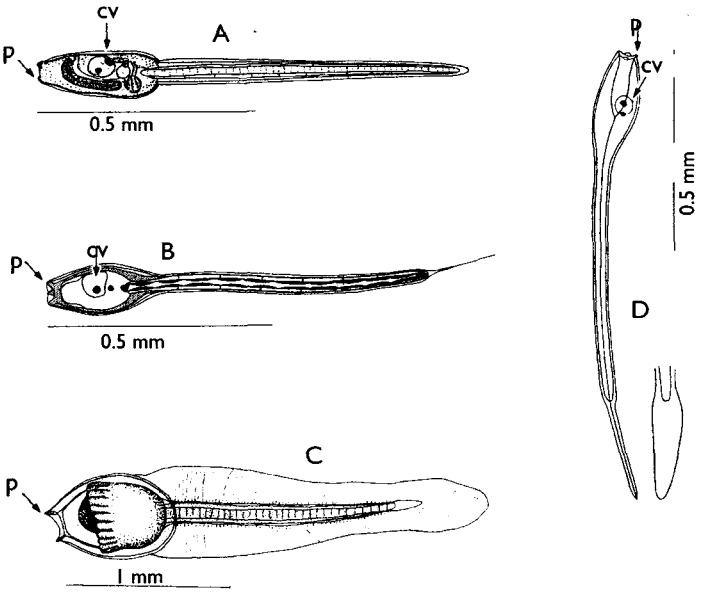

Fig. 5. Solitary ascidian larvae: (A) ***Ciona intestinalis***. (B) ***Boltenia villosa***. (C) ***Metandrocarpa taylori***. (D) ***Styela*** sp. Species or genera found locally are in bold. Abbreviations: adhesive papillae (p), cerebral vesicle (cv). (A from Berrill, 1947, Fig. 1; B from Cloney, 1961, Plate 1-1; C from Abbott, 1955, Fig. 1; D from Grave, 1944, Fig. 1)

family or genus. At present, the only way to identify a larval type to species is to raise larvae to the adult stage. See Strathmann (1987) for information on culturing larvae.

Relatively few characteristics are available to key ascidian larvae without difficult dissections and tissue analysis. Easily observed morphological characteristics such as color, length, and shape of trunk are useful when differentiating between solitary and colonial ascidian larvae. To distinguish among the less differentiated solitary ascidian larvae usually requires closer examination through a compound microscope to examine the cuticular layers of the trunk tunic and the attached test cells. All ascidian larvae have two cuticular layers of tunic (Fig. 4), but the inner cuticular layer is absent in the tail of some species. The larvae of some species of solitary ascidian have prominent, firmly attached test cells on the outer cuticular

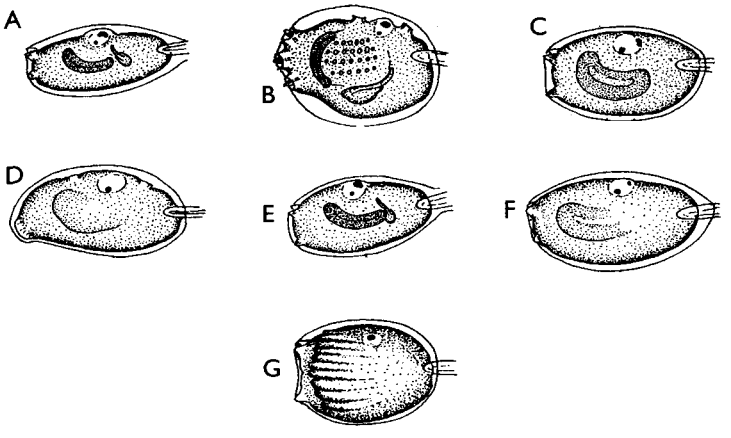

Fig. 6. Larvae of solitary ascidians (tails not shown). (A) ***Ciona intestinalis***. (B) ***Perophora*** *listeri*. (C) ***Pyura*** *microcosmus*. (D) ***Molgula*** *citrina*. (E) ***Ascidia*** *mentula*. (F) ***Styela*** *partita*. (G) ***Dendrodoa*** *grossularia*. Species or genera found locally in bold. Figures not to scale. (From Millar, 1971, Fig. 5)

Table 1. Diagnostic information for solitary ascidian species

Species	*Mean Length (mm)*	*Color*	*Tail with Inner Cuticular Layer*[1]	*Attached Test Cells*[1]
Order Pleurogona				
Suborder Phlebobranchia				
Family Cionidae				
Ciona intestinalis	1.1	Transparent	+	+
Family Perophoridae				
Perophora annectens		Transparent	+	+
Family Corellidae				
Chelyosoma columbianum				
Chelyosoma productum	1.2	Transparent	+	+
Corella inflata	0.9	Transparent	+	+
Corella willmeriana	0.9	Transparent	+	+
Family Ascidiidae				
Ascidia callosa	1.2	Transparent	-	+
Ascidia paratropa	1.2	Transparent	-	+
Ascidia prunum	1.2	Transparent	-?	+
Ascidia ceretodes	1.2	Transparent	-?	+
Suborder Stolidobranchia				
Family Styelidae				
Cnemidocarpa finmarkiensis		Pale Rose, Orange	+	-
Dendrodoa abbotti		Transparent		
Metandrocarpa dura	2.5			
Metandrocarpa taylori		Vermillion		
Styela clavata			+	-
Styela coriacea	1.1	Orange	+	-
Styela gibbsii		Orange	+	-
Styela montereyensis		Orange		
Styela truncata				
Styela (barnharti) clava		Orange		
Family Pyuridae				
Boltenia villosa	0.8-1.2	Transparent	+	-
Halocynthia aurantium	1.5	Pale Yellow	+	-
Halocynthia igaboja	1.5-1.9	Pale Yellow	+	-
Pyura haustor	1.6	Transparent	+	-
Pyura mirabilis				
Family Molgulidae				
Molgula cooperi			-?	-
Molgula manhattensis	0.7		-?	-
Molgula oregonia			-?	-
Molgula pacifica			-?	-
Molgula pugetiensis			-?	-

1 Presence of character: + = yes; - = no.

layer of tunic which are visible under a compound microscope (Burighel and Cloney, 1997).

Solitary Ascidians

All solitary ascidian larvae are small (<1.5 mm length) and have relatively simple internal structures (Figs. 5, 6). All but the family Molgulidae have three simple attachment papillae with a coniform shape and a triangular configuration (see Fig. 5). The Molgulidae lack attachment papillae. *Ciona intestinalis* and all species from the family Ascidiidae have firmly attached test cells on the outer cuticular layer of tunic. The inner cuticular layer of the tunic is absent in the tail of the following species: *Corella inflata, Chelyosoma productum, Ascidia callosa, A. paratropa* (probably all ascidiids), and *Molgula occidentalis* (probably all molgulids) (R. A. Cloney, pers. comm.) (see Fig. 4). *Corella* and *Chelyosoma* species have trunks compressed in the sagittal plane. *Halocynthia* species have long trunks that taper down in

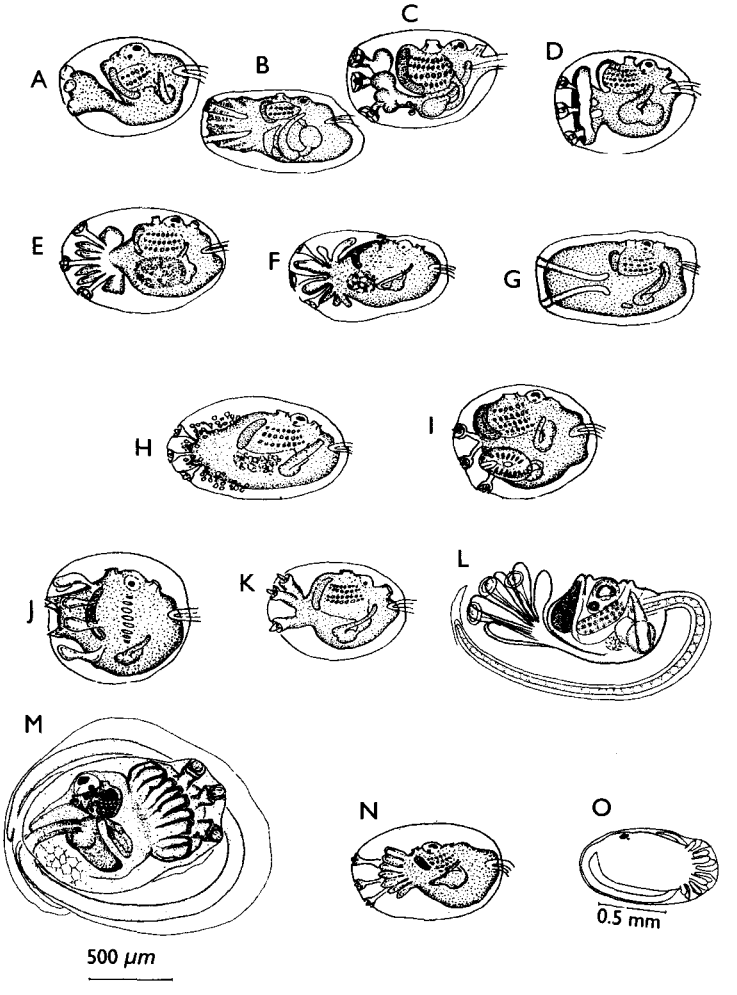

Fig. 7. Larvae of compound ascidians. (A) ***Clavelina*** *lepadiformis*. (B) ***Pycnoclavella stanleyi***. (C) ***Distaplia*** *rosea*. (D) ***Cystodytes*** *dellechiajei*. (E) ***Eudistoma*** *illotum*. (F) ***Synoicum*** *georgianum*. (G) ***Euherdmania claviformis***. (H) ***Apidium*** *nordamanni*. (I) ***Diplosoma listerianum***. (J) ***Botrylloides*** *leachi*. (K) *Sycozoa sigillinoides*. (L) ***Archidistoma*** *aggregatum*. (M) ***Didemnum albidum***. (N) ***Didemnum*** *helgolandicum*. (O) ***Ritterela rubra***. Species or genera found locally are in bold. Figures A-L, N are not to scale. (A–K, N from Millar, 1971, Fig. 5; L from Berrill, 1948, Fig. 2; M from Marks 1996, Fig. 4A; O from Abbott and Trason, 1968, Fig. 1C)

diameter toward the papillae. All other species listed have trunks that are round to ovoid in cross section at the middle of the trunk. Additional diagnostic information on other solitary species is compiled in Table 1.

Table 2. Diagnostic information for compound ascidian larvae

Species	*Length (mm)*	*Color*	*Adhesive Papillae*		*Tail Twisted Counter-Clockwise*
			Shape[1]	*Configuration*	
Order Enterogona					
Suborder Aplousobranchia					
Family Clavelinidae					
Archidistoma molle					
Archidistoma psammion					
Eudistoma ritteri	3.0				
Eudistoma purpuropunctatum			Scy	Sagittal	
Clavelina huntsmani		Orange	Scy	Sagittal	
Clavelina sp.					
Cystodytes lobatus					
Distaplia occidentalis	3.2		Scy	Triangle	+
Distaplia smithi			Scy	Triangle	+
Pycnoclavella stanleyi			T-inv		
Family Polyclinidae					
Aplidium arenatum	2.5		Goblet	Sagittal	
Aplidium californicum	2.5		Goblet	Sagittal	
Aplidium glabrum	2.5		Goblet	Sagittal	
Aplidium propinquum	2.5		Goblet	Sagittal	
Aplidium solidum	2.5		Goblet	Sagittal	
Aplidium sp.	2.5		Goblet	Sagittal	
Euherdmania claviformis	3.0		T-inv		+
Ritterella aequalisiphonis					
Ritterella pulchra					
Ritterella rubra	0.8				
Synoicum parfustis					
Synoicum sp.					
Family Didemnidae					
Didemnum albidum	2.7				
Didemnum carnulentum					
Diplosoma listerianum	2.4		Scy	Sagittal	+
Tridemnum opacum					
Tridemnum strangulatum					
Suborder Stolidobranchia					
Family Styelidae					
Botrylloides sp.			Sim		
Botryllus sp.	1.5		Scy	Triangle	

[1]Scy = scyphate, the papillae appear to be set in cup-shaped invaginations in the trunk (e.g., Distaplia, see Fig. 2); T-inv = inverted (invaginated) tubular papillae that extend deeply into the body cavity of the trunk (e.g., Pycnoclavella, Fig. 7B); Goblet = goblet-shaped papillae with elongate tubular stalks (e.g., Aplidium, Fig. 7H).

Compound Ascidians

All larvae from colonial ascidians are greater than 1.5 mm in length and have relatively complex internal structures. All have three adhesive papillae except *Euherdmania claviformis*, which has two. Additional diagnostic characteristics of the larvae of local colonial ascidians are compiled in Table 2, and compound ascidian larvae are illustrated in Fig. 7.

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