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Nemertea: The Ribbon Worms

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Nemerteans are an ancient group of worms derived from the flat worms. Worldwide, there are about 800 species in the phylum Nemertea. They are found at all depths in the ocean, as well as in some freshwater and damp terrestrial habits, and a few species are commensals. Locally there are 39 species (Table 1).

The nemerteans are characterized by soft, elongate, and non-segmented bodies that are covered with cilia. Their bodies are highly contractile, a characteristic for which they are famous; intertidal species that when contracted are around 8 cm long can be 45 cm long when fully extended (Haderlie, 1980). Nemerteans are predators, capturing prey with a unique eversible proboscis that can be shot out to capture a victim.

Reproduction and Development

The phylum Nemertea displays a wide variety of reproductive strategies. Many species are dioecious, though cases of hermaphroditism have been observed (Stricker, 1987). Although the ability to regenerate the body is common (e.g., Nusbaum and Oxner, 1910, 1911), asexual reproduction is not a normal part of the reproductive cycle for most nemerteans. Fertilization is often external. Eggs may either be spawned freely into the water column, protected in a gelatinous egg mass or other encasement, or, in a few instances, held internally by species that are ovoviviparous.

The development of most nemerteans (orders Palaeonemertea, Hoplonemertea, and Bdellonemertea) appears to be direct, with wormlike (vermiform) young developing in benthic egg cases before hatching. According to Stricker (1987), vermiform juvenile nemerteans typically remain on the benthos after hatching, but some may spend a brief period in the plankton. Cantell (1989), however, in listing known life histories of fourteen "direct" developing species, defines half as "pelagic." Also, there seems to be confusion about whether to call vermiform, adult-like young "larvae" or "juveniles" (this problem is not unique to nemerteans). Some experts use the term "larva" when referring to pelagic, but apparently direct-developing forms (e.g., Iwata, 1960a, 1968; Cantell, 1989). Others, however, consider the hoplonemerteans, palaeo-

nemerteans, and bdellonemerteans to undergo more traditional direct development and to lack a larval stage altogether (e.g., Stricker, 1987; Brusca and Brusca, 1990). These different points of view may arise from conflicting reports about whether the epithelium of pre-settling nemerteans is shed during "metamorphosis" (Stricker and Reed, 1981). Most palaeonemerteans, hoplonemerteans, and bdellonemerteans, whether undergoing pelagic or benthic development, are thought to develop from the embryo directly into the oval, ciliated vermiform stage, which proceeds to the benthic juvenile *without* shedding the epithelium. Because the post-embryonic young of palaeonemerteans, hoplonemerteans, and bdellonemerteans are adult-like in form and undergo no dramatic metamorphosis, I refer to them as juveniles.

The fourth order of nemerteans, the Heteronemertea, often undergo indirect development with a pelagic stage known as a pilidium larva. The pilidium larva looks like a helmet or hat, with ciliated lobes for locomotion and capturing food particles. Others exhibit a Desor's larval stage and develop within a benthic egg case. *Micrura akkeshiensis* passes through the Iwata larval stage (Iwata, 1958), which is similar in certain respects to a pilidium larva but lacks the lobes and helmet shape. Additional details on the reproductive biology of nemerteans are available in Cantell (1989).

Identification of Regional Taxa

Table 1 summarizes species and developmental modes of nemerteans thought to be found in the Pacific Northwest (Coe, 1905; Austin, 1985; Stricker, 1996). The Nemertea are continuously undergoing extensive taxonomic revision. Consequently, Coe (1905) and more recent observations are most useful with knowledge of synonymies and recent taxonomic changes (see Gibson, 1995). It should be noted that developmental life history in the majority of species found in the Pacific Northwest is unknown. In these cases, information in this chapter provides the developmental modes of taxonomically related species with the caution that developmental life history cannot be confidently stated until directly observed for the species in question.

Orders Palaeonemertea, Hoplonemertea, and Bdellonemertea

Juveniles of the orders Palaeonemertea (class Anopla), Hoplonemertea (class Enopla), and Bdellonemertea (class Enopla) are generally wormlike and develop directly into the

Table 1. Species in the phylum Nemertea from the Pacific Northwest (taxonomic authority from Gibson, 1995)

<i>Taxa</i>	<i>Development</i> ^a
Class Anopla	
Order Heteronemertea	
<i>Cerebratulus albifrons</i>	Pilidium (genus)
<i>Cerebratulus californiensis</i>	Pilidium (Coe, 1940)
<i>Cerebratulus herculeus</i>	Pilidium (genus)
<i>Cerebratulus marginatus</i>	Pilidium (Coe, 1905)
<i>Cerebratulus montgomeryi</i>	Pilidium (genus)
<i>Cerebratulus occidentalis</i>	Pilidium (genus)
<i>Lineus pictifrons</i>	Pilidium-like or benthic direct (genus)
<i>Lineus ruber</i>	Desor's (Gontcharoff, 1960)
<i>Lineus bilineatus</i>	Pilidium (Cantell, 1989)
<i>Lineus rubescens</i>	Pilidium-like or benthic direct (genus)
<i>Micrura alaskensis</i>	Pilidium (Stricker & Folsom, 1998)
<i>Micrura verrilli</i>	Pilidium (Coe, 1940)
<i>Micrura wilsoni</i>	Pilidium (genus)
<i>Myosiphagos sanguineus</i>	Pilidium-like or benthic direct (order)
Order Palaeonemertea	
<i>Carinoma mutabilis</i>	Direct, pelagic not specified (Coe, 1940)
<i>Carinomella lactea</i>	Pelagic direct (genus)
<i>Procephalothrix spiralis</i>	Pelagic direct (family)
<i>Tubulanus capistratus</i>	Pelagic direct (genus)
<i>Tubulanus polymorphus</i>	Pelagic direct (Stricker, 1987)
<i>Tubulanus sexlineatus</i>	Pelagic direct (genus)
Class Enopla	
Order Hoplonemertea	
<i>Amphiporus angulatus</i>	Pelagic or benthic direct (order)
<i>Amphiporus bimaculatus</i>	Pelagic or benthic direct (order)
<i>Amphiporus cruentatus</i>	Pelagic or benthic direct (order)
<i>Amphiporus formidabilis</i>	Pelagic or benthic direct (order)
<i>Amphiporus imparispinosus</i>	Pelagic or benthic direct (order)
<i>Carcinonemertes epialti</i>	Pelagic direct (Stricker & Reed, 1981)
<i>Carcinonemertes errans</i>	Pelagic direct (genus)
<i>Emplectonema buergeri</i>	Pelagic direct (genus)
<i>Emplectonema gracile</i>	Pelagic direct (Stricker & Cloney, 1982)
<i>Nemertopsis gracilis</i>	Pelagic direct (family)
<i>Oerstedtia dorsalis</i>	Pelagic direct (Gontcharoff, 1961)
<i>Paranemertes peregrina</i>	Pelagic direct (Roe, 1976)
<i>Tetrastemma nigrifrons</i>	Benthic direct (genus)
<i>Tetrastemma candidum</i>	Benthic direct (genus)
<i>Tetrastemma phyllospadicola</i>	Benthic direct (Stricker, 1985)
<i>Zygonemertes virescens</i>	Pelagic or benthic direct (order)
Order Bdeionemertea	
<i>Malacobdella grossa</i>	Pelagic direct (Hammarsten, 1918)
<i>Malacobdella siliquae</i>	Pelagic direct (genus)
<i>Malacobdella macomae</i>	Pelagic direct (genus)

^aIf development has not been studied, then the development of the closest relative is given (shared taxonomic level in parentheses). Species for which the development is known are in bold.

adult nemertean. These juveniles are typically elongate, covered with short cilia, and may bear an apical tuft of long cilia. Additional tufts of long cilia, but shorter than the apical tuft, may be present at the posterior or paired in anteriolateral positions. Direct development has been attributed to eight local species (see Table 1). Some general descriptions of juvenile appearance are published. For instance, the juvenile of *Oerstedia dorsalis* is milky white in color, has two pairs of ocelli, and may be 0.43 mm in length at hatching (Iwata, 1960a). Bear in mind, however, that attributes such as color, size, and ocelli number are probably only superficially descriptive, and undescribed juveniles may possess the same traits. Consequently, no information is currently available with which the many vermiform nemertean juveniles may be confidently distinguished. To provide an idea of their general appearance, Fig. 1 gives examples of pelagic hoplonemertean and palaeonemertean juvenile forms from around the world.

Some claim it is possible to distinguish between palaeonemertean juveniles and other vermiform juveniles on the basis of the presence or absence of a functional proboscis. According to Iwata (1960b), palaeonemerteans do not develop a functional proboscis until after "metamorphosis," whereas enoplans (especially hoplonemerteans) possess a proboscis in the pelagic stage and use it to capture prey. An example of a proboscis is given in Fig. 2. Cantell (1989) points out, however, that Jägersten (1972) observed an apparently functional proboscis in the palaeonemertean *Cephalothrix*. Therefore, caution should be used before assigning a juvenile to an order based solely on the presence or absence of a proboscis. Also, Iwata (1960a) states that the larve of many hoplonemertean and bdellonemertean

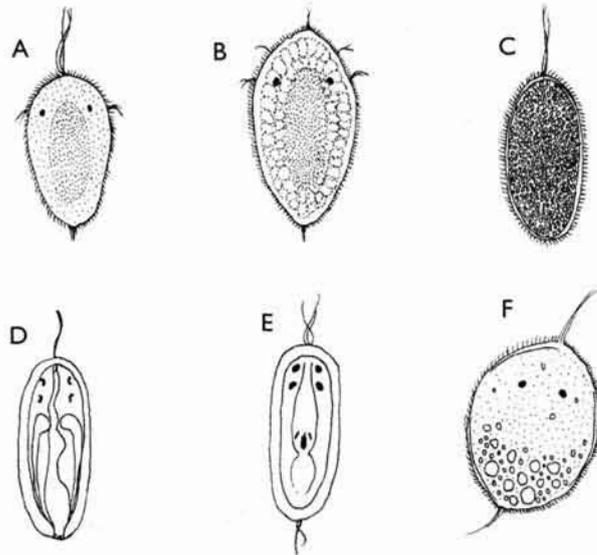
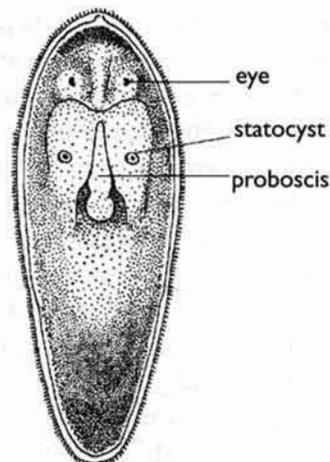


Fig. 1. Oval-shaped vermiform pelagic juveniles of palaeonemerteans (A-C) and hoplonemerteans (D-F). A, *Procephalothrix filiformis*; B, *Procephalothrix simulus*; C, *Tubulanus* sp.; D, *Oerstedia dorsalis*; E, *Emplectonema gracile*; F, *Carcinonemertes* sp. Two species from the Pacific Northwest are shown: *Oerstedia dorsalis* and *Emplectonema gracile* (D, E). (A, E adapted from Iwata, 1960a; B, C adapted from Iwata, 1968; D adapted from Gontcharoff, 1961; F adapted from Humes, 1942)

Fig. 2. Unidentified pelagic nemertean juvenile from the west coast of Sweden, bearing "larval" proboscis (PR). EY, eye; ST, statocyst; length = 0.6 mm. Statocysts are present in relatively few species. (after Jägersten, 1972)



species are elliptical and have long anterior and short posterior tufts. As can be seen from Fig. 1, however, palaeonemerteans can also be elliptical in shape and possess similar ciliary patterns.

Order Heteronemertea

Nemerteans of the order Heteronemertea primarily display indirect development with a planktonic pilidium larva. Based on known development of congeners (see Table 1), local heteronemerteans without a pilidium larva probably either undergo benthic direct development or pass through a Desor's larval stage within an egg case.

Four genera of heteronemerteans are found along the coast of the Pacific Northwest: *Cerebratulus*, *Lineus*, *Micrura*, and *Myoisophagos*. The latter genus is represented in the region by the heteronemertean previously known as *Lineus vegetus*, which was recently synonymized with *Myoisophagos sanguineus* (Riser, 1994). Development has been studied for only six of the region's heteronemertean species, one of which possesses a Desor's larva and has no pelagic phase. Reviewed below are examples of pilidium larvae from the genera *Cerebratulus*, *Lineus*, and *Micrura*. Sources for these adapted illustrations do not always clearly indicate the larval size; in such cases, size is not indicated. On the basis of personal observations of Oregon coast pilidium larvae, it seems that pilidium length is commonly between 0.2 and 1.5 mm, depending on stage and species.

Local representatives of genera are used as examples below when possible, but most illustrations are of species from outside the Pacific Northwest. These diagrams are provided to show the range of pilidium form. As more is learned about

the local pilidium larvae, it may be possible to create a key that uses a combination of size, pigment patterns, and lobe patterns to assign pilidium larvae to genus or species. This system has been suggested (Cantell, 1969) for Swedish coast pilidium larvae (see further discussion at end of chapter).

Genus *Cerebratulus*. It is thought that all members of the genus *Cerebratulus* produce a planktonic pilidium larva. This is indeed the case for the two local *Cerebratulus* species studied, *C. marginatus* (Fig. 3) and *C. californiensis*. *Cerebratulus* larvae tend to be large (>1 mm in height) and have a pyramidal shape (a pointed apex). Larvae depicted in Fig. 3 lack a pointed apex, possibly because of distortion due to preservation (Fig. 3A) or because they are too young to display the mature larval shape (Fig. 3B). *Cerebratulus* pilidium larvae sometimes possess subdivided lobes (e.g., Fig. 3A) that are distinct from the lobes of other heteronemertean genera.

Genus *Lineus*. *Lineus bilineatus* is found on the Pacific Northwest coast and is known to produce a pilidium larva. In contrast, *Lineus ruber*, also found locally, produces a benthic, encased Desor's larva. Members of this genus may also develop directly in egg cases, free-living on the benthos, or in the water column. Advanced *Lineus* pilidium larvae so far described tend to be smaller than the larvae of *Cerebratulus* species (i.e., <1 mm in height), bear a rounded apex and episphere, and have continuous lobes with no subdivision (T. Lacalli, pers. comm.). Examples of pilidium larvae from this genus, both collected along the coast of Japan, are given in Fig. 4.

Genus *Micrura*. *Micrura*, the least-studied of the pilidium-producing genera, is represented by three species in the Pacific Northwest. Two of these species are known to produce a pilidium larva, *M. alaskensis* (Stricker and Folsom, 1998) and *M. verrilli* (Coe, 1940). No illustrations of local *Micrura* larvae are available, and I am unable to locate any good descriptions of advanced pilidium larva from this genus. The illustration

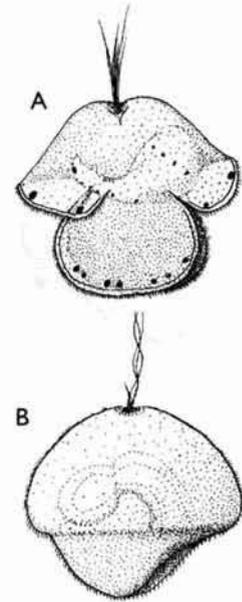


Fig. 3. (A) Advanced *Cerebratulus lacteus* pilidium larva; shape of apex possibly distorted by preservation. (B) Ten-day-old pilidium larva of *Cerebratulus marginatus*, a species found on the Oregon coast; this larva is probably too young and indistinct to differentiate it from the pilidium larvae of other heteronemertean species and genera. (A adapted from Verrill, 1892; B adapted from Coe, 1905)

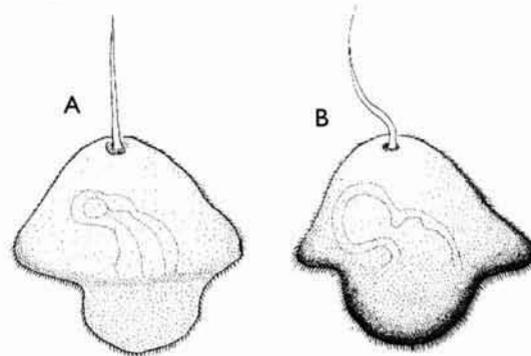


Fig. 4. (A) Pilidium larva of *Lineus torquatus*, body height without apical tuft = 0.24 mm. (B) Pilidium larva of *Lineus alborostratus*, body height without apical tuft = 0.3 mm. (A adapted from Iwata, 1957; B adapted from Iwata, 1960a)

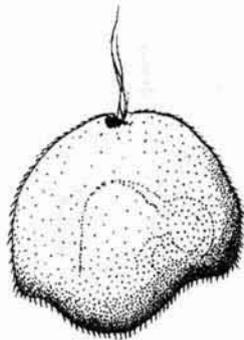


Fig. 5. Pilidium larva of *Micrura leidy*; this larva is likely too young and indistinct to be differentiated from the pilidium larvae of other heteronemertean species and genera. (adapted from Coe, 1943)

of an early pilidium from the New England coast presented here (Fig. 5), an adaptation of one of the few published drawings of a *Micrura* pilidium larva, is too young and indistinct to be differentiated from other heteronemertean pilidium larvae.

Characteristics distinguishing the pilidium larvae in Figs. 3–5 may not be consistent characteristics of their genera. It does appear, however, that advanced *Cerebratulus* pilidium larvae tend to be relatively large, exceeding 1 mm in height, have a pointed apex, and sometimes have subdivided lobes, whereas advanced *Lineus* larvae tend to be smaller and more regular in shape (see Fig. 4 for examples). Until useful observations are made of the advanced larvae of unstudied heteronemerteans, however, this should be viewed only as a provocative pattern in need of validation. Observations are especially needed of *Micrura* species, for which little or no information is available on the advanced pilidium larva. Many detailed studies of nemertean development must be completed before the pilidium larvae found off the Pacific Northwest can be related confidently to species.

History of Pilidium Larva Classification

More than a century ago the first attempts were made to classify pilidium larvae (Bürger, 1895). For pilidium larvae in the Gulf of Naples, Bürger used traits such as shape of the helmet, shape of the lateral lobes, and length of the apical ciliary tuft. In addition to using these traits, Schmidt (1937) presented a method of identifying pilidium larvae that stressed the size ratio between lobes and placed pilidium larvae into descriptive groups. Dawydoff (1940) also classified pilidium larvae in descriptive groups, using names that indicate larval morphology such as *Pilidium elongatum*, *P. magnum*, *P. minutum*, *P. longivertex*, and *P. depressum*. Cantell (1969) points out that larval groupings such as these can embrace species of different families, are therefore not natural taxonomic units, and should probably be avoided. Cantell also provides the most recent attempt to link pilidium larvae with their corresponding adults and uses a more modern view of nemertean relationships. Characteristics used by Cantell to describe pilidium larvae found off the west coast of Sweden include helmet shape, lateral lobe shape, apical tuft length, body size, pigmentation, and planktonic season. He argues convincingly that, taken together, these traits can provide information on pilidium identity. Characteristics of imaginal juveniles, visible within some transparent pilidium larvae, and newly metamorphosed (hatched) heteronemerteans may also provide clues to larval

taxonomy. These characteristics include eye placement and color, head shape, cephalic furrows, and presence or absence of the caudal cirrus (tail).

Development is undescribed for the majority of the local heteronemertean species. As more observations are made on nemertean development, it will be possible to relate pilidium larvae to their respective adults using morphology, pigmentation, and temporal distribution of the larvae. Too little information is currently available to apply Cantell's (1969) system even at the genus level. Riser's observation in 1974 that our knowledge was too incomplete to relate pilidium larvae to adult species is still very true for most pilidium larvae in the world, including those of the Pacific Northwest.

Making New Observations

Indeed, more information is needed about the development of many nemertean species. For those making new observations on pilidium larvae, whether on lab-reared or field-caught animals, the following thoughts and tips are provided to help make observations most useful. Common problems associated with describing pilidium larvae arise from descriptions of fixed specimens or very young larvae, morphologically indistinct from other species.

As with all zooplankton, specimens are best observed alive. This is especially important for the soft-bodied pilidium larvae, because the helmet-like form is easily distorted by muscle contractions during fixation. For instance, *Cerebratulus* pilidium larvae typically have a pointed apex, being rather pyramidal in shape. The pilidium larva of *C. lacteus*, adapted from Verrill (1892) and depicted in Fig. 3A, probably possesses a more pointed apex that has been distorted by muscle contraction in the fixation process. Contraction of muscles not only distorts shape but can make the larva appear smaller than its actual size. It is best, if possible, to collect a wide range of sizes and developmental stages. This helps the observer know how large the larvae can get before they are ready to metamorphose. Finally, two points regarding collection and preservation: First, when samples are fixed, it is wise to sort quickly and separate soft-bodied forms, such as pilidium larvae, from the rest of the sample; this can prevent further damage in a vial or jar of settled plankton. Second, plankton tows for soft-bodied forms should be gentle, preferably towed by hand and using a blind cod-end (Reeve, 1981). This guards against the distortion of delicate forms caused by water flowing forcefully through the plankton net.

Many available illustrations depict young pilidium larvae, which are morphologically indistinct from the pilidium larvae of other species (e.g., Figs. 3B, 5). These early, undifferentiated pilidium larvae are often raised from the fertilized eggs of adults in the laboratory. This yields the significant advantage of knowing the identity of the parents, but the pilidium larvae must be raised to a late, mature stage to be distinct. Attempts to raise pilidium larvae to later stages have been largely unsuccessful, possibly because of improper suspension in the culture vessel or ignorance of the appropriate diet. Pilidium larvae caught in the field are often more advanced developmentally, but the identity of the adult may not be known. It is possible to raise newly metamorphosed juvenile nemerteans, captured as advanced pilidium larvae in the plankton, to the point where the species can be identified. The diet of juvenile nemerteans is better understood than that of planktonic pilidium larvae; attempts to raise juvenile worms can meet with some success. The important point, however, is that descriptions of pilidium larvae should include the most advanced distinct stages possible.

Acknowledgments

The author expresses sincere appreciation to the following experts, who shared their knowledge and contributed immensely to this project: R. Gibson of the Liverpool John Moores University, S. A. Stricker of the University of New Mexico at Albuquerque, T. Lacalli of the University of Saskatchewan, and F. Iwata of the Akkeshi Marine Biological Station, Hokkaido.

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