

LESSER-KNOWN INVERTEBRATES: THE LOPHOPHORATES, ENTOPROCTS, CYCLIOPHORES, AND CHAETOGNATHS

THE LOPHOPHORATES: BRACHIOPODA, ECTOPROCTA (BRYOZOA), AND PHORONIDA

Three of the phyla (Brachiopoda, Ectoprocta [Bryozoa], and Phoronida) discussed in this endpaper share one major anatomical feature—the **lophophore** (Gr. *lophos*, crest or tuft + *phorein*, to bear). The lophophore is a circumoral (around the mouth) body region characterized by a circular or U-shaped ridge, with either one or two rows of ciliated, hollow tentacles (figure 1). An anus always opens outside of the lophophore. The lophophore is a food-collecting organ and a surface for gas exchange. Sensory cells receptive to chemicals and touch are concentrated on its tentacles. The lophophore can usually be extended for feeding or withdrawn for protection.

All lophophorates are sessile or sedentary filter feeders that have a U-shaped digestive tract—a feature common in sedentary animals—and live in a secreted chitinous or calcareous tube. As in deuterostomes, these phyla have radial cleavage in embryonic stages and a coelom that is divided into compartments. As in protostomes, however, the embryonic mouth forms in the region of the blastopore. Recent molecular biological studies involving the sequencing of ribosomal DNA, however, suggest that the lophophorates are protostomes.

PHYLUM BRACHIOPODA: THE BRACHIOPODS, OR LAMPSHELLS

The brachiopods (brak-i-op'ods) (Gr. *brachion*, arm + *podos*, foot) bear a superficial resemblance to the bivalve molluscs because they have a bivalved, calcareous and/or chitinous shell that a mantle secretes and that encloses nearly all of the body. However, unlike the left and right valves in molluscs, the brachiopods have dorsal and ventral valves. In addition, molluscs filter with their gills, whereas brachiopods use a lophophore. Brachiopods are commonly called lampshells because they resemble ancient Roman oil lamps.

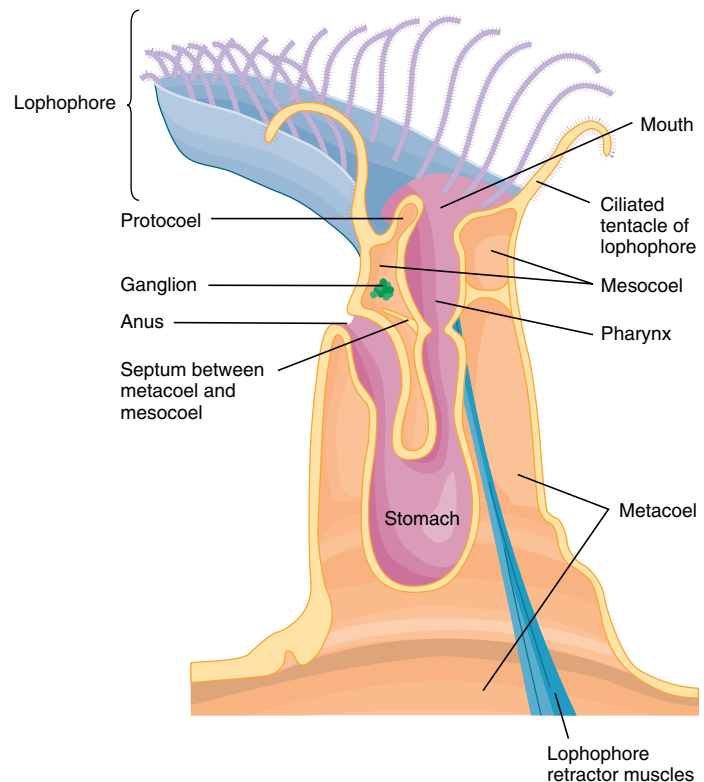


FIGURE 1 Lophophorate Structure. Longitudinal section through the body of a lophophorate with the lophophore extended. Miller/Harley: *Zoology*, 5th ed. © The McGraw-Hill Companies.

Brachiopods are exclusively marine; most species live from the tidal zone to the edge of the continental shelves (about 200 m deep). The phylum contains about three hundred living species. In the Articulata, the valves are composed primarily of calcium carbonate and have a hinge with interlocking teeth (figure 2). The Inarticulata have unhinged valves that are composed primarily of calcium phosphate and held together only by muscles. Most members of both classes have a stalked pedicel that usually attaches to a hard surface. Some, such as *Lingula*, have a muscular pedicel used for burrowing and anchoring in mud or sand.

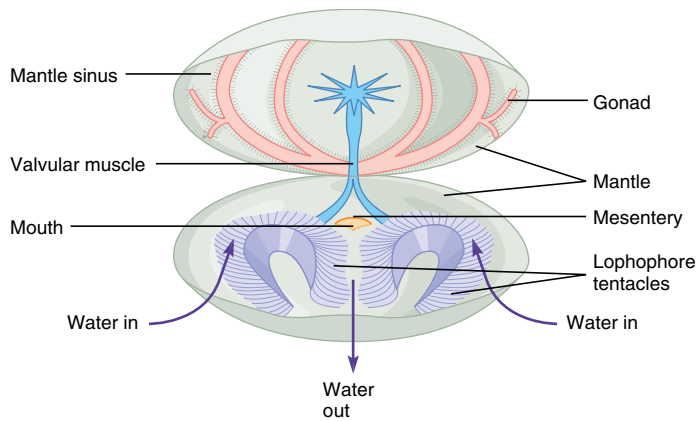


FIGURE 2 Phylum Brachiopoda. Internal anatomy of an articulate brachiopod. Miller/Harley: *Zoology*, 5th ed. © The McGraw-Hill Companies.

The large, horseshoe-shaped lophophore in the anterior mantle cavity bears long, ciliated tentacles used in respiration and feeding (figure 2). The cilia set up water currents that carry food particles (mainly organic detritus and algae) between the valves and over the lophophore into the mouth.

A solitary, dioecious brachiopod reproduces sexually by releasing gametes from multiple gonads into the metacoel and discharging them into the water by the nephridia. Fertilization is usually external, and the nonfeeding, ciliated, free-swimming larva is planktonic before settling and developing into an adult. Development is similar to that of deuterostomes, with radial, mostly equal, holoblastic cleavage, and enterocoelous coelom formation. In the Inarticulata, the juvenile resembles a small brachiopod with a coiled pedicel in the mantle cavity. There is no metamorphosis; when the juvenile settles to the bottom, the pedicel attaches to a solid object, and adult existence begins.

PHYLUM ECTOPROCTA (BRYOZOA): MOSS ANIMALS

The ectoprocts (ek'to-proks) (Gr. *ektos*, outside + *proktos*, anus) or bryozoans superficially resemble hydroids or corals. Bryozoa (Gr. *bryon*, moss + *zoon*, animal) means moss animals and refers to the mosslike appearance of the colonies. The name ectoprocta refers to the position of the anus outside the ring of tentacles. The approximately four thousand living species of pseudocoelomate ectoprocts belong to three classes. All species are aquatic (both freshwater and marine) and less than 1.5 mm in length.

Each body, or zooid, has a circular or horseshoe-shaped lophophore and is covered with a thin cuticle that encloses a calcified exoskeleton (see figure 1). The feeding body (lophophore, digestive tract, muscles, nerves) is called the polypide, the exoskeleton plus body wall (epidermis) is the cystid, and the secreted, nonliving part (exoskeleton) is the zoecium (Gr. *zoo*, animal + *oceus*, house). Ectoprocts have an eversible lophophore that can be withdrawn into the body. Contraction of the retractor muscle rapidly withdraws the lophophore, whereas contraction of the muscles encircling the body wall exert pressure on the coelomic fluid, everting the lophophore.

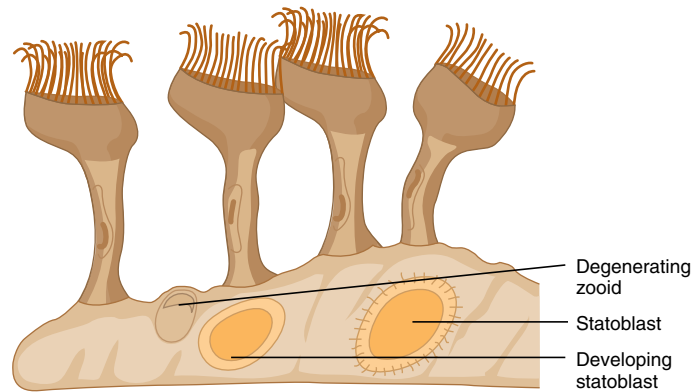


FIGURE 3 Phylum Ectoprocta. An ectoproct colony forming statoblasts. Miller/Harley: *Zoology*, 5th ed. © The McGraw-Hill Companies.

Ectoprocts grow by budding. Thin portions of the body wall grow out as small vesicles or tubes, and contain a complete zooid. The different budding patterns reflect the genetics of the individual animal and such factors as current flow and substrate. The factors determine the colony shape (e.g., thin sheets, convoluted folds, massive coral-like heads, upright tangles). Each colony can contain about 2 million zooids.

Most ectoprocts are monoecious. In some species, heterozooids produce either eggs or sperm in different colonies. In others, simple gonads produce both sperm and eggs in the same autozooid. Sperm enter the coelomic cavity, exit through pores in the tips of the tentacles, and are caught by the tentacles of other colonies. Eggs are fertilized as they are released and are brooded in the coelom; some species have a modified ovicell in which the embryo develops. Marine species have radial cleavage and a free-swimming, ciliated larva. This larva swims for a variable period of time, depending on the species, and then sinks and attaches to a rock or other substrate and grows into a zooid. A colony forms by budding.

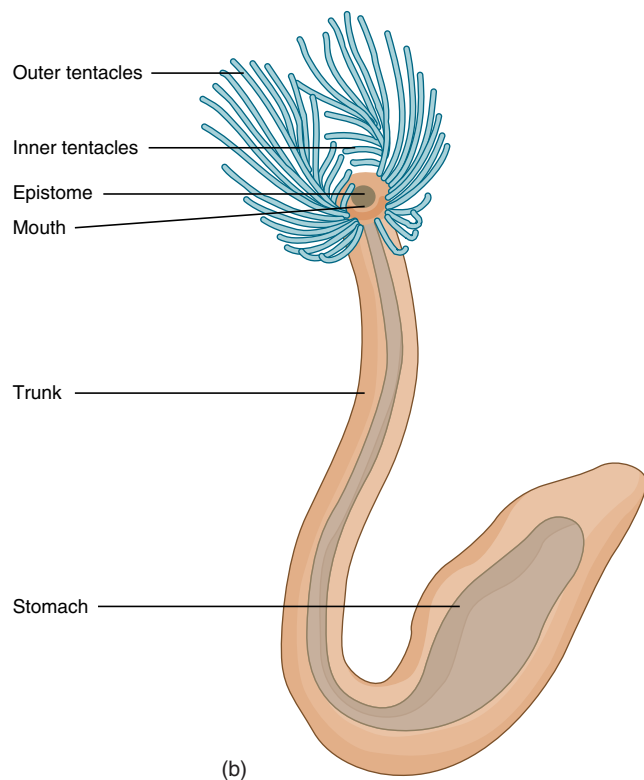
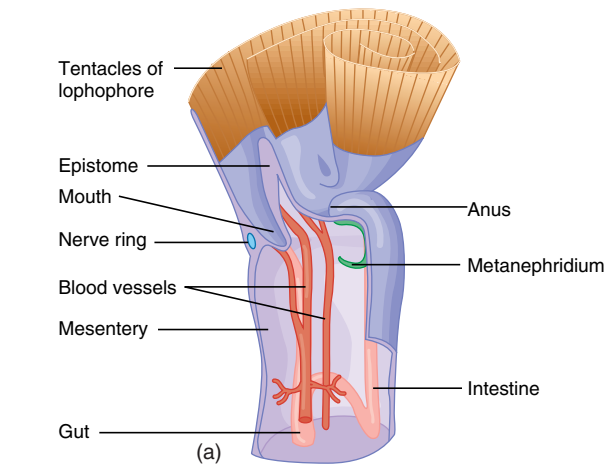
Some freshwater ectoprocts produce a dormant stage called a statoblast (figure 3). A statoblast is a hard, resistant capsule containing a mass of germinative cells. Statoblasts are asexually produced and accumulate in the metacoel. They can survive long periods of freezing and drying, enabling a colony to survive many years in seasonally variable lakes and ponds. Some float and are carried downstream, or are blown or carried from pond to pond, spreading ectoprocts over a large area. When environmental conditions become favorable, the statoblasts hatch and give rise to new polypides and, eventually, new colonies.

PHYLUM PHORONIDA: THE PHORONIDS

The Phoronids (fo-ron'ids) consist of about a dozen marine species divided between two genera: *Phoronis* and *Phoronopsis*. These animals live in permanent, chitinous tubes either buried in muddy or sandy sediments, or attached to solid surfaces. A few species bore into mollusc shells or calcareous rock. Generally, only the tentacles extend into the overlying water. Most phoronids are small—less than 20 cm long.

The adult phoronid body consists of an anterior lophophore with two parallel rings of long tentacles (figure 4). The tentacles of the lophophore are filled with coelomic fluid that serves as a hydrostatic skeleton to hold them upright. The cilia on the tentacles drive water into the ring of tentacles from the top of the lophophore and out through the narrow spaces between the tentacles. Suspended food particles are directed toward the mouth. A flap of tissue called the epistome (Gr. *epi*, around + *stome*, mouth) covers the mouth.

Some phoronids reproduce asexually by budding and transverse fission; however, the majority are hermaphroditic. The gonads are in the coelom. Gametes pass from the coelom through the nephridiopore to the tentacles. Cross-fertilization is the rule,



and the zygotes are either protected among the coils of the lophophore or released into the sea. Cleavage is radial, and a free-swimming larva called the actinotroch develops and feeds on plankton while drifting in the sea. It eventually settles to the bottom, metamorphoses, and begins to grow ventrally to form the body of the sedentary adult. As the animal grows, it burrows into the substrate. The body wall contains gland cells that eventually secrete the chitinous tube.

NONLOPHOPHORATE PHyla

The phyla Entoprocta and Cycliophora lack lophophores but share other similarities with the lophophorates. As discussed at the conclusion of this endpaper, some zoologists think that all five phyla —Brachiopoda, Ectoprocta, Phoronida, Endoprocta, and Cycliophora— have evolutionary ties.

PHYLUM ENTOPROCTA

The entoprocts (en'to-proks) (Gr. *entos*, within + *proktos*, anus) comprise a small phylum of about one hundred species of sedentary marine filter feeders. They are either solitary or colonial, and live in coastal waters. One group is commensalistic on the body surface of various invertebrates. Most entoprocts are microscopic. Entoprocts may form large, matlike colonies on rocks. An individual entoproct consists of a muscular stalk bearing a cup-shaped calyx with a crown of ciliated tentacles (figure 5). The stalk is sur-

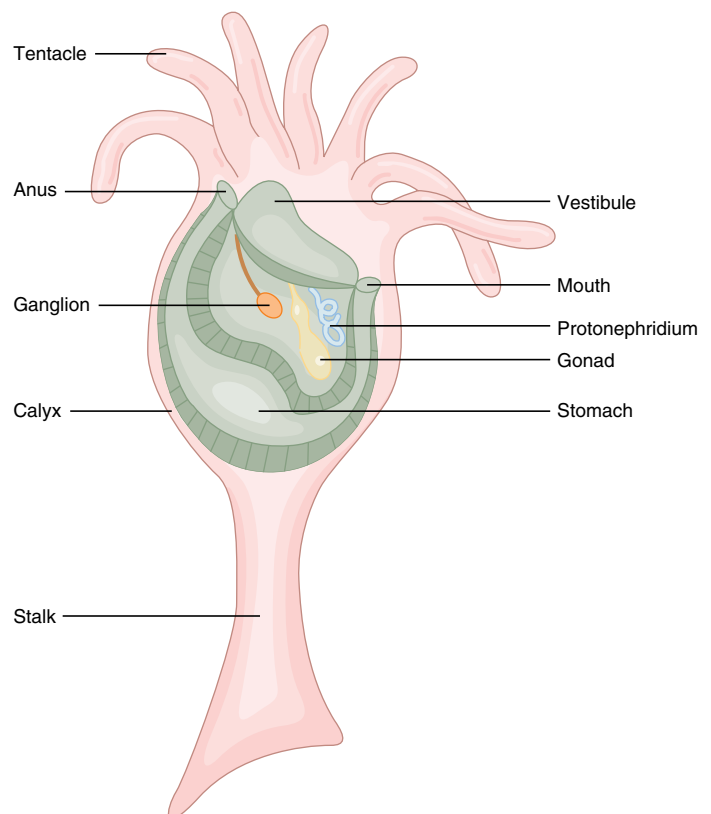


FIGURE 4 Phylum Phoronida. (a) Longitudinal view of the internal anatomy of the anterior portion of a phoronid. (b) A phoronid removed from its tube. Miller/Harley: *Zoology*, 5th ed. © The McGraw-Hill Companies.

FIGURE 5 Phylum Entoprocta. Some morphological features of a typical entoproct. Miller/Harley: *Zoology*, 5th ed. © The McGraw-Hill Companies.

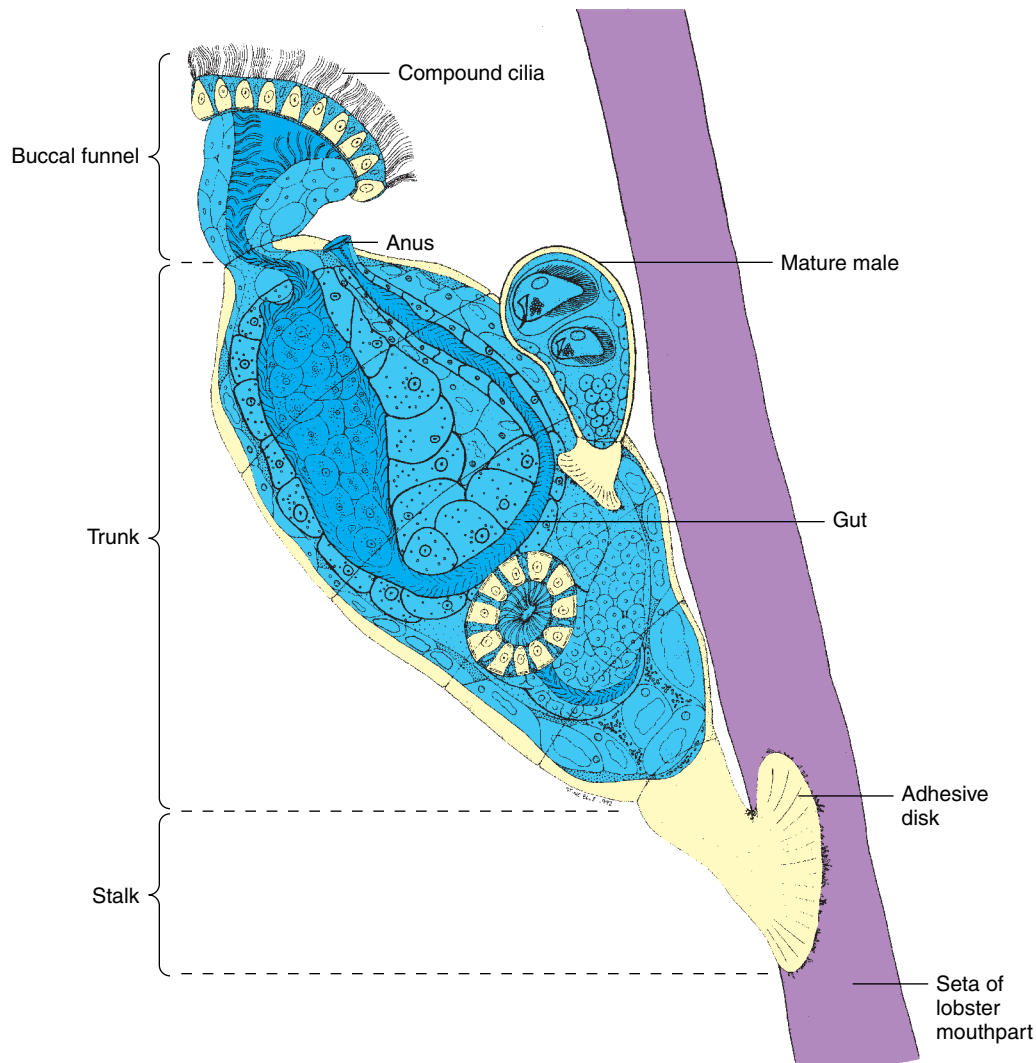


FIGURE 6 *Phylum Cycliophora.* The feeding stage of *Symbion pandora* attaches to the seta of the mouthpart of a lobster. A mature male is shown attached to the feeding stage, which is about 300 μm (0.3 mm) long. Miller/Harley: *Zoology*, 5th ed. © The McGraw-Hill Companies.

rounded by a chitinous cuticle and may bear an attachment disk with adhesive glands.

Entoprocts have a small body cavity that most zoologists consider a pseudocoelom. Loose connective tissue, however, fills this body cavity. How this cavity forms and its function are not well known. These uncertainties contribute to questions regarding the phylogenetic position of this group.

Entoprocts are filter feeders, and cilia on the tentacles convey food into the mouth. The filter-feeding apparatus is similar to the lophophore described for three previous phyla. The entoproct feeding structure, however, is not a lophophore because the anus ends with the group of tentacles. Lophophores, by definition, have an anal opening outside their ring of tentacles. The digestive tract forms a U-shaped gut in the calyx. Also in the calyx is a pair of protonephridial tubules that open through a single pore in the mouth. The nervous system consists of a small, central ganglion and radiating nerves. Gas exchange occurs across the body surface.

Entoprocts reproduce by asexual budding and also sexually. Most entoprocts are monoecious, but eggs and sperm usually are produced at different times in one animal. Sperm are released freely into the water, and fertilization occurs internally. Embryos develop in a brood chamber, from which free-swimming larvae are released. Eventually, larvae settle to the substrate and develop into adults.

PHYLUM CYCLOPHORA

As mentioned in chapter 7, P. Funch and R. M. Kristensen described the phylum Cycliophora (si''kle-o-for'ah) (Gr. *cyclion*, small wheel + *phora*, to carry) in 1995. It is the most recently described animal phylum. Members of its single species (*Symbion pandora*) are acoelomate, marine, and bilaterally symmetrical. They live in association with the mouthparts of lobsters.

The body of the feeding stage of *Symbion* consists of a buccal funnel, a trunk, and a stalk that ends in an adhesive disk. The disk attaches to a seta on the mouthparts of the lobster host (figure 6;

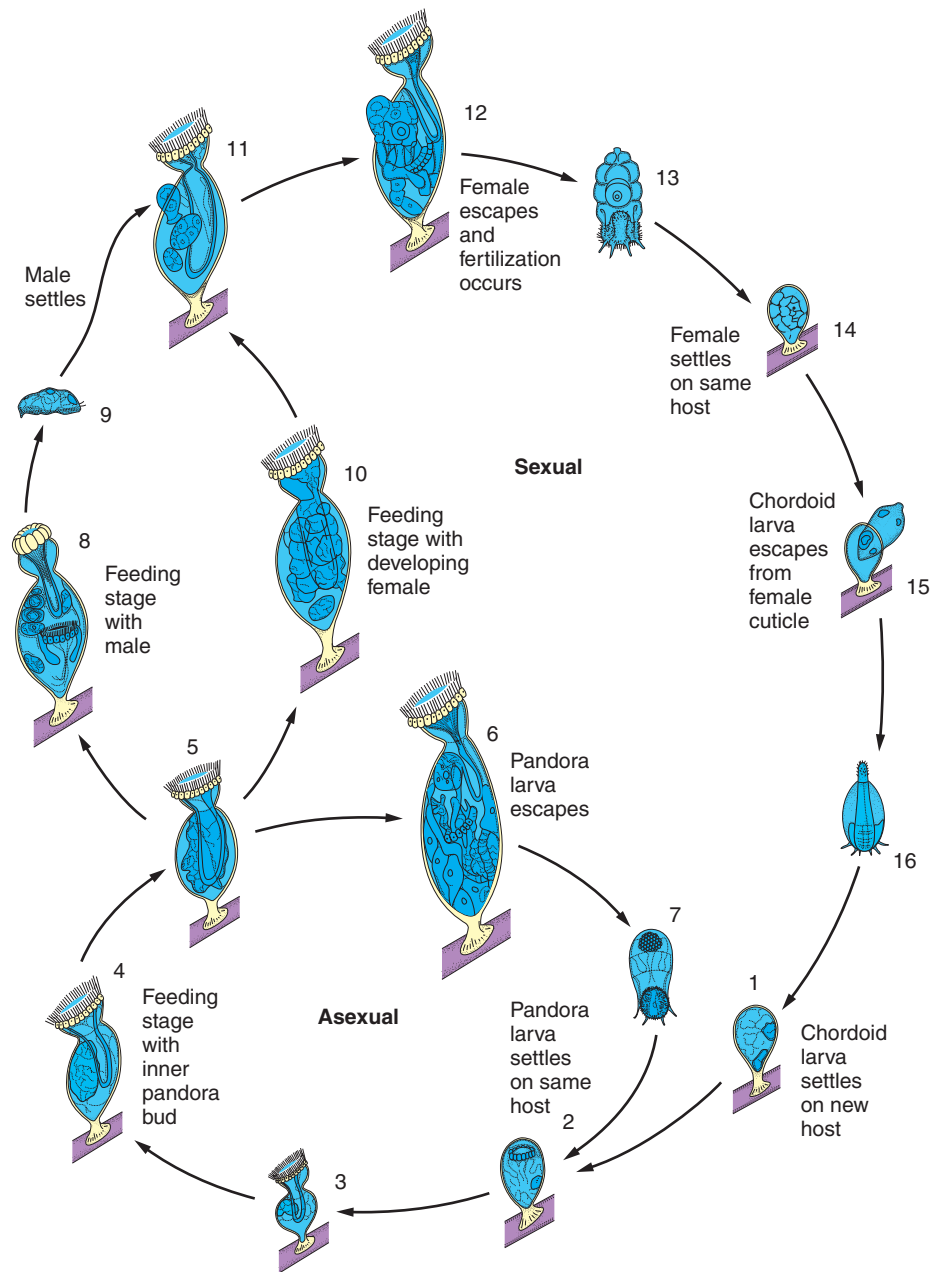


FIGURE 7 Life Cycle of *Symbion pandora*. The feeding stage of *Symbion* undergoes an asexual reproductive phase (1 & 7) that involves the development of a pandora larval stage that escapes from the feeding adult and settles on the mouthparts of the same lobster host. It matures and begins feeding. Prior to a molt by the lobster, feeding individuals form males or females within their body (8-10). When a male matures, it escapes from its feeding parent and attaches to a feeding stage containing a maturing female (9 & 11). When the female matures it escapes from its feeding parent, fertilization occurs, and the female settles on the same lobster host (12). The female then dies, but she leaves her cuticle containing a chordoid larva attached to the lobster mouthpart. When the larva is mature, it breaks out of the cuticle, swims through the water, and may find a new host lobster (13-16). Miller/Harley: *Zoology*, 5th ed. © The McGraw-Hill Companies.

see figure 7). The buccal funnel contains the mouth and is surrounded by a ring of compound cilia used in filter feeding. A cuticle lines the body on the outside. The mouth leads to a U-shaped gut tract. Protonephridia are used in excretion.

Figure 7 shows the life cycle of *Symbion* that Funch and Kristensen proposed. The asexual feeding stage is about 0.3 mm tall. It can reproduce asexually by producing a larval stage, called the pandora, that is released and settles on the same host. Because of this asexual reproduction, large numbers of *Symbion* can build up

on one host. After settling and attachment, the new individual develops a buccal funnel and begins to feed.

Sexual reproduction is apparently correlated to the molt cycle of the lobster. Some cue, possibly hormonal, from the lobster signals *Symbion* that the lobster is about to molt. Male and female stages are produced within the bodies of feeding individuals. When it is mature and filled with sperm, a male escapes from its maternal feeding individual and settles on a feeding individual containing a maturing female. As the female escapes from its ma-

ternal feeding individual, fertilization occurs, and the female settles on the lobster's mouthparts. The female contains a single, large fertilized egg. The female dies, leaving a cuticular shell containing a chordoid larva. The chordoid larva is the dispersal stage. It is free-swimming and may settle on the mouth appendages of a new lobster host.

PHYLUM CHAETOGNATHA: THE ARROW WORMS

Members of the phylum Chaetognatha (ke"tog-nath'ah) (Gr. *chaite*, hair or bristle + *gnathos*, jaw) are the arrow worms. The approximately one hundred species in this phylum are distributed throughout the world's oceans. Most are planktonic, 0.5 to 12 cm in length, streamlined, bilaterally symmetrical, and nearly transparent. Their body consists of a head, trunk, and tail (figure 8). The trunk has paired, lateral fins, and the tail has a single fin. The mouth is located ventrally on the head. Large, grasping spines are lateral to the mouth, and smaller spines, called teeth, are in front of the mouth.

Arrow worms are active swimmers. The near-perfect bilateral symmetry and streamlined shape of arrow worms permit a darting form of locomotion from laterally flexing the body. Their fins stabilize the body during swimming and help prevent sinking during moments of rest.

Arrow worms are active predators. They feed on planktonic crustaceans and small fish. An arrow worm darts forward quickly to grab its prey with mouth spines that inject a neurotoxic venom into the prey. Interestingly, the neurotoxin is not produced by the arrow worm, but by commensalistic bacteria living in the head region. The gut of arrow worms is a simple, straight tube. Although much remains to be learned about arrow worm physiology, circulation, gas exchange, and excretion probably all occur by diffusion. The nervous system consists of a cerebral ganglion in the head and other ganglia associated with sensory organs. Ciliary fans that cover the body probably detect waterborne vibrations. A single pair of eyes is below the epidermis on the dorsal surface of the head. Arrow worms probably use these photoreceptors to orient to the direction and intensity of light during vertical migrations within the water column.

Chaetognaths are monoecious, with paired ovaries in the trunk and paired testes in the tail. Arrow worms engage in a mating dance during which they deposit sperm in ball-like clusters on the mate's body. These sperm clusters rupture, and sperm migrate to the female gonopore. Fertilization is internal, and zygotes in a jellylike coating float in the sea or sink to the substrate. One genus has a marsupial pouch within which fertilized eggs develop. There is no larval stage or metamorphosis.

PHYLOGENETIC RELATIONSHIPS

The evolutionary relationships among the six phyla described in this endpaper are controversial. The traditional interpretation is

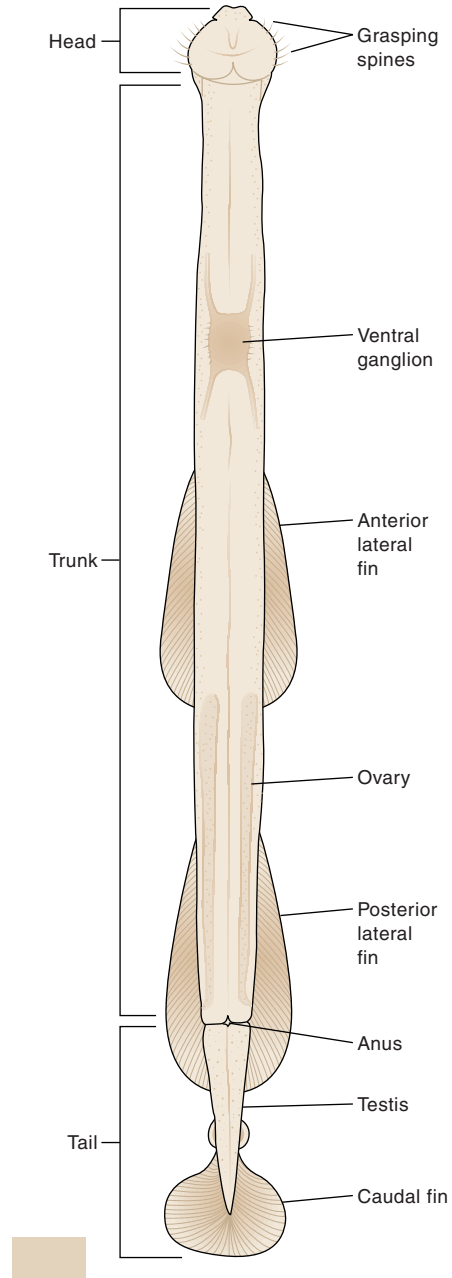


FIGURE 8 Arrow Worm. Ventral view of *Parasagitta* (2 to 3 cm). Miller/Harley: *Zoology*, 5th ed. © The McGraw-Hill Companies.

that the lophophore of the Brachiopoda, Ectoprocta (Bryozoa), and Phoronida represents an evolutionary tie among these three phyla. More recent molecular studies of ribosomal RNA seem to support this view. Other similarities, such as a reduced head, U-shaped digestive tract, and secreted protective covering, correlate with adaptations for a sessile, filter-feeding existence. These common features may represent evolutionary convergence, rather than close evolutionary relationships. This traditional interpretation would mean that the ectoprocts and cyclophores are more

distantly related to the lophophorates. Because of what appears to be a pseudocoelom, the entoprocts are often considered as helminths.

C. Nielsen has recently suggested that the ectoprocts and entoprocts are closely related. He advocates a superphylum designation, Bryozoa, to reflect this relationship. Funch and Kristensen suggest that the Cycliophora have affinities to these "Bryozoa." They point to such common features as a certain kind of protonephridium (Entoprocta and Cycliophora), budding (Entoprocta, Ectoprocta, and Cycliophora), disappearance of the larval brain at metamorphosis (Entoprocta, Ectoprocta, and Cyclio-

phora), and other common characters as indications of close evolutionary ties. Although this interpretation has not been widely accepted, discussions of the phylogenetic status of these five phyla (Brachiopoda, Ectoprocta, Phoronida, Endoprocta, and Cycliophora) will probably become more frequent and interesting as a result of the discovery of *Symbion*.

Very little is known regarding the phylogenetic relationships of the Chaetognatha. Their embryological development clearly indicates that they are deuterostomes. Their relationships to other deuterostomes are highly speculative.