

# 45

## *Mollusks and Annelids*

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### Concept Outline

#### 45.1 Mollusks were among the first coelomates.

**Coelomates.** Next to the arthropods, mollusks comprise the second most diverse phylum and include snails, clams, and octopuses. There are more terrestrial mollusk species than terrestrial vertebrates!

**Body Plan of the Mollusks.** The mollusk body plan is characterized by three distinct sections, a unique rasping tongue, and distinctive free-swimming larvae also found in annelid worms.

**The Classes of Mollusks.** The three major classes of mollusks are the gastropods (snails and slugs), the bivalves (oysters and clams), and the cephalopods (octopuses and squids). While they seem very different at first glance, on closer inspection, they all have the same basic mollusk body plan.

#### 45.2 Annelids were the first segmented animals.

**Segmented Animals.** Annelids are segmented coelomate worms, most of which live in the sea. The annelid body is composed of numerous similar segments.

**Classes of Annelids.** The three major classes of annelids are the polychaetes (marine worms), the oligochaetes (earthworms and related freshwater worms), and the hirudines (leeches).

#### 45.3 Lophophorates appear to be a transitional group.

**Lophophorates.** The three phyla of lophophorates share a unique ciliated feeding structure, but differ in many other ways.



**FIGURE 45.1**

**An annelid, the Christmas-tree worm, *Spirobranchus giganteus*.** Mollusks and annelids inhabit both terrestrial and aquatic habitats. They are large and successful groups, with some of their most spectacular members represented in marine environments.

Although acoelomates and pseudocoelomates have proven very successful, a third way of organizing the animal body has also evolved, one that occurs in the bulk of the animal kingdom. We will begin our discussion of the coelomate animals with mollusks, which include such animals as clams, snails, slugs, and octopuses. Annelids (figure 45.1), such as earthworms, leeches, and seaworms, are also coelomates, but in addition, were the earliest group of animals to evolve segmented bodies. The lophophorates, a group of marine animals united by a distinctive feeding structure called the lophophore, have features intermediate between those of protostomes and deuterostomes and will also be discussed in this chapter. The remaining groups of coelomate animals will be discussed in chapters 46, 47, and 48.

## 45.1 Mollusks were among the first coelomates.

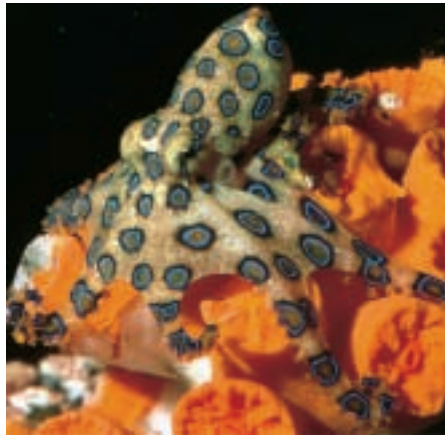
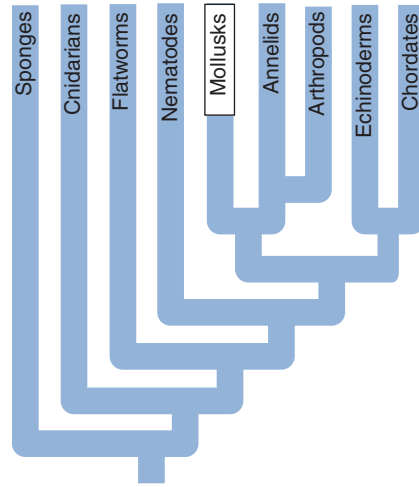
### Coelomates

The evolution of the *coelom* was a significant advance in the structure of the animal body. Coelomates have a new body design that repositions the fluid and allows the development of complex tissues and organs. This new body plan also made it possible for animals to evolve a wide variety of different body architectures and to grow to much larger sizes than acoelomate animals. Among the earliest groups of coelomates were the mollusks and the annelids.

### Mollusks

Mollusks (phylum Mollusca) are an extremely diverse animal phylum, second only to the arthropods, with over 110,000 described species. Mollusks include snails, slugs, clams, scallops, oysters, cuttlefish, octopuses, and many other familiar animals (figure 45.2). The durable shells of some mollusks are often beautiful and elegant; they have long been favorite objects for professional scientists and amateurs alike to collect, preserve, and study. Chitons and nudibranchs are less familiar marine mollusks. Mollusks are characterized by a coelom, and while there is extraordinary diversity in this phylum, many of the basic components of the mollusk body plan can be seen in figure 45.3.

Mollusks evolved in the oceans, and most groups have remained there. Marine mollusks are widespread and often abundant. Some groups of mollusks have invaded freshwater and terrestrial habitats, including the snails and slugs that live in your garden. Terrestrial mollusks are often abundant in places that are at least seasonally moist. Some of these places, such as the crevices of desert rocks, may appear very dry, but even these habitats have at least a temporary supply of water at certain times. There are so many terrestrial mollusks that only the arthropods have more species adapted to a terrestrial way of life. The 35,000 species of terrestrial mollusks far outnumber the roughly 20,000 species of terrestrial vertebrates.



**FIGURE 45.2**  
A mollusk. The blue-ringed octopus is one of the few mollusks dangerous to humans. Strikingly beautiful, it is equipped with a sharp beak and poison glands—divers give it a wide berth!

As a group, mollusks are an important source of food for humans. Oysters, clams, scallops, mussels, octopuses, and squids are among the culinary delicacies that belong to this large phylum. Mollusks are also of economic significance to us in many other ways. For example, pearls are produced in oysters, and the material called mother-of-pearl, often used in jewelry and other decorative objects, is produced in the shells of a number of different mollusks, but most notably in the snail called abalone. Mollusks are not wholly beneficial to humans, however. Bivalve mollusks called shipworms burrow through wood submerged in the sea, damaging boats, docks, and pilings. The zebra mussel has recently invaded North American ecosystems from Europe via the ballast water of cargo ships from Europe, wreaking havoc in many aquatic ecosystems. Slugs and terrestrial snails often cause extensive damage to garden flowers, vegetables, and crops. Other mollusks serve as hosts to the intermediate stages of many serious parasites, including several nematodes and flatworms, which we discussed in chapter 44.

Mollusks range in size from almost microscopic to huge, although most measure a few centimeters in their largest dimension. Some, however, are minute, while others reach formidable sizes. The giant squid, which is occasionally cast ashore but has rarely been observed in its natural environment, may grow up to 21 meters long! Weighing up to 250 kilograms, the giant squid is the largest invertebrate and, along with the giant clam (figure 45.4), the heaviest. Millions of giant squid probably inhabit the deep regions of the ocean, even though they are seldom caught. Another large mollusk is the bivalve *Tridacna maxima*, the giant clam, which may be as long as 1.5 meters and may weigh as much as 270 kilograms.

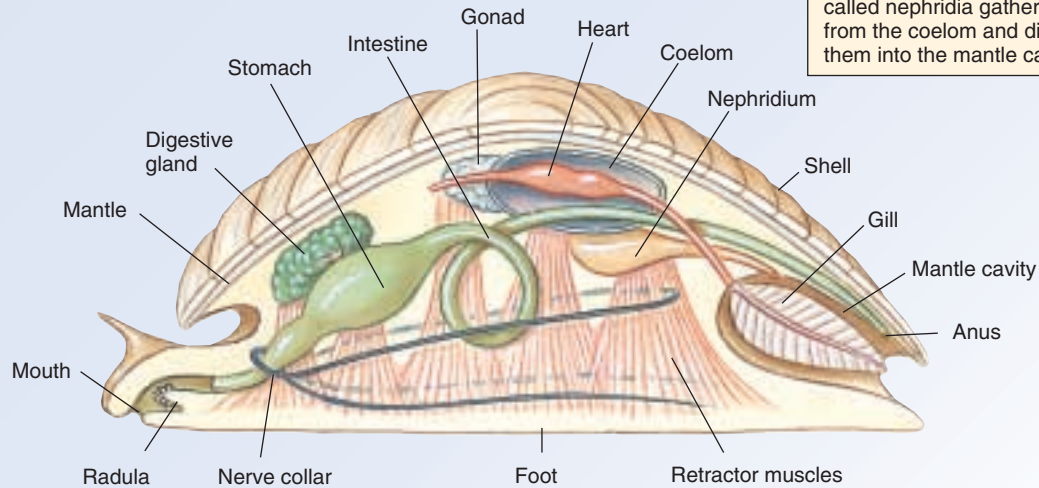
**Mollusks are the second-largest phylum of animals in terms of named species; mollusks exhibit a variety of body forms and live in many different environments.**

# PHYLUM MOLLUSCA: Coelom

The mantle is a heavy fold of tissue wrapped around the mollusk body like a cape. The cavity between the mantle and the body contains gills, which capture oxygen from the water passing through the mantle cavity. In some mollusks, like snails, the mantle secretes a hard outer shell.

Snails have a three-chambered heart and an open circulation system. The coelom is confined to a small cavity around the heart.

Mollusks were among the first animals to develop an efficient excretory system. Tubular structures called nephridia gather wastes from the coelom and discharge them into the mantle cavity.



Many mollusks are carnivores. They locate prey using chemosensory structures. Within the mouth of a snail are horny jaws and a unique rasping tongue called a radula.

Snails creep along the ground on a muscular foot. Squid can shoot through the water by squeezing water out of the mantle cavity, in a kind of jet propulsion.

**FIGURE 45.3**

**Evolution of the coelom.** A generalized mollusk body plan is shown above. The body cavity of a mollusk is a coelom, which is completely enclosed within the mesoderm. This allows physical contact between the mesoderm and the endoderm, permitting interactions that lead to development of highly specialized organs such as a stomach.

**FIGURE 45.4**

**Giant clam.** Second only to the arthropods in number of described species, members of the phylum Mollusca occupy almost every habitat on earth. This giant clam, *Tridacna maxima*, has a green color that is caused by the presence of symbiotic dinoflagellates (zooxanthellae). Through photosynthesis, the dinoflagellates probably contribute most of the food supply of the clam, although it remains a filter feeder like most bivalves. Some individual giant clams may be nearly 1.5 meters long and weigh up to 270 kilograms.



## Body Plan of the Mollusks

In their basic body plan (figure 45.5), mollusks have distinct bilateral symmetry. Their digestive, excretory, and reproductive organs are concentrated in a **visceral mass**, and a muscular **foot** is their primary mechanism of locomotion. They may also have a differentiated **head** at the anterior end of the body. Folds (often two) arise from the dorsal body wall and enclose a cavity between themselves and the visceral mass; these folds constitute the **mantle**. In some mollusks the mantle cavity acts as a lung; in others it contains gills. **Gills** are specialized portions of the mantle that usually consist of a system of filamentous projections rich in blood vessels. These projections greatly increase the surface area available for gas exchange and, therefore, the animal's overall respiratory potential. Mollusk gills are very efficient, and many gilled mollusks extract 50% or more of the dissolved oxygen from the water that passes through the mantle cavity. Finally, in most members of this phylum, the outer surface of the mantle also secretes a protective shell.

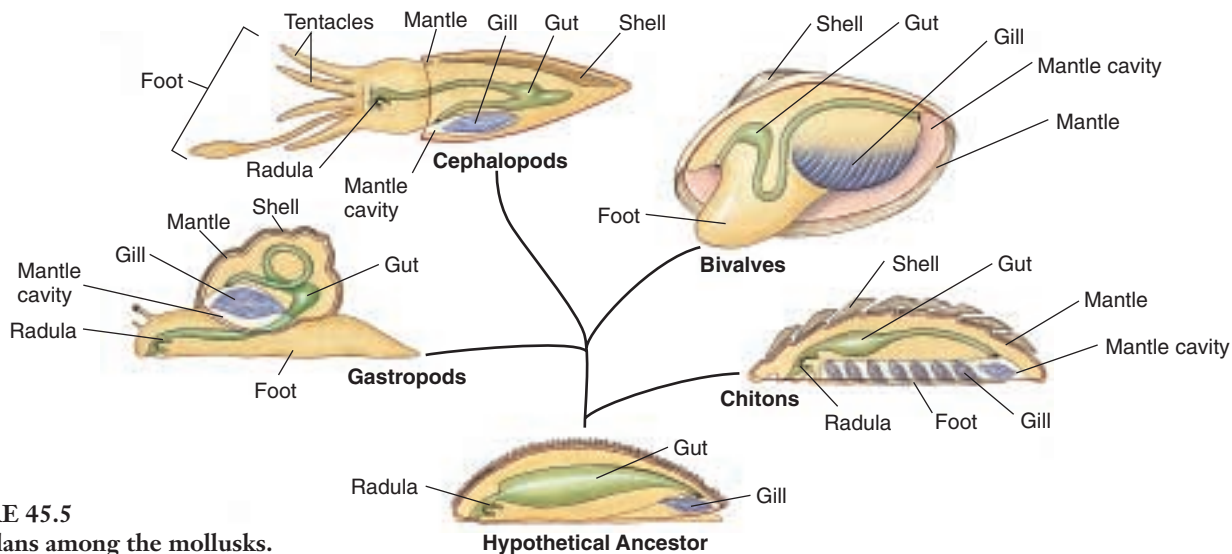
A mollusk shell consists of a horny outer layer, rich in protein, which protects the two underlying calcium-rich layers from erosion. The middle layer consists of densely packed crystals of calcium carbonate. The inner layer is pearly and increases in thickness throughout the animal's life. When it reaches a sufficient thickness, this layer is used as mother-of-pearl. Pearls themselves are formed when a foreign object, like a grain of sand, becomes lodged between the mantle and the inner shell layer of **bivalve mollusks** (two-shelled), including clams and oysters. The mantle coats the foreign object with layer upon layer of shell material to reduce irritation caused by the object. The shell of mollusks serves primarily for protection. Many species can withdraw for protection into their shell if they have one.

In aquatic mollusks, a continuous stream of water passes into and out of the mantle cavity, drawn by the cilia on the gills. This water brings in oxygen and, in the case of the bivalves, also brings in food; it also carries out waste materials. When the gametes are being produced, they are frequently carried out in the same stream.

The foot of a mollusk is muscular and may be adapted for locomotion, attachment, food capture (in squids and octopuses), or various combinations of these functions. Some mollusks secrete mucus, forming a path that they glide along on their foot. In cephalopods—squids and octopuses—the foot is divided into arms, also called tentacles. In some *pelagic* forms, mollusks that are perpetually free-swimming, the foot is modified into wing-like projections or thin fins.

One of the most characteristic features of all the mollusks except the bivalves is the **radula**, a rasping, tongue-like organ used for feeding. The radula consists primarily of dozens to thousands of microscopic, chitinous teeth arranged in rows (figure 45.6). Gastropods (snails and their relatives) use their radula to scrape algae and other food materials off their substrates and then to convey this food to the digestive tract. Other gastropods are active predators, some using a modified radula to drill through the shells of prey and extract the food. The small holes often seen in oyster shells are produced by gastropods that have bored holes to kill the oyster and extract its body for food.

The circulatory system of all mollusks except cephalopods consists of a heart and an open system in which blood circulates freely. The mollusk heart usually has three chambers, two that collect aerated blood from the gills, while the third pumps it to the other body tissues. In mollusks, the coelom takes the form of a small cavity around the heart.



**FIGURE 45.5**  
Body plans among the mollusks.

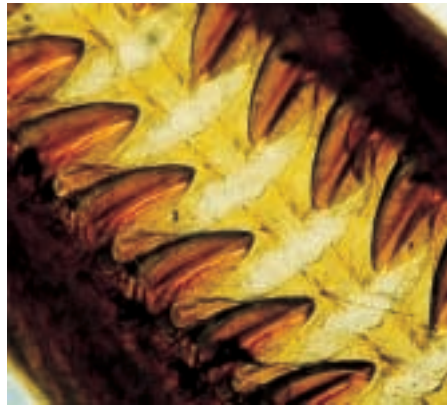
Nitrogenous wastes are removed from the mollusk by one or two tubular structures called **nephridia**. A typical nephridium has an open funnel, the **nephrostome**, which is lined with cilia. A coiled tubule runs from the nephrostome into a bladder, which in turn connects to an excretory pore. Wastes are gathered by the nephridia from the coelom and discharged into the mantle cavity. The wastes are then expelled from the mantle cavity by the continuous pumping of the gills. Sugars, salts, water, and other materials are reabsorbed by the walls of the nephridia and returned to the animal's body as needed to achieve an appropriate osmotic balance.

In animals with a closed circulatory system, such as annelids, cephalopod mollusks, and vertebrates, the coiled tubule of a nephridium is surrounded by a network of capillaries. Wastes are extracted from the circulatory system through these capillaries and are transferred into the nephridium, then subsequently discharged. Salts, water, and other associated materials may also be reabsorbed from the tubule of the nephridium back into the capillaries. For this reason, the excretory systems of these coelomates are much more efficient than the flame cells of the acoelomates, which pick up substances only from the body fluids. Mollusks were one of the earliest evolutionary lines to develop an efficient excretory system. Other than chordates, coelomates with closed circulation have similar excretory systems.

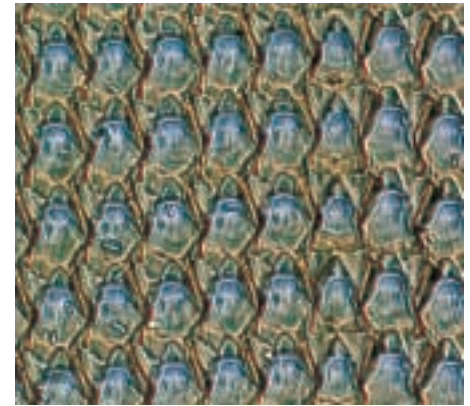
## Reproduction in Mollusks

Most mollusks have distinct male and female individuals, although a few bivalves and many gastropods are hermaphroditic. Even in hermaphroditic mollusks, cross-fertilization is most common. Remarkably, some sea slugs and oysters are able to change from one sex to the other several times during a single season.

Most aquatic mollusks engage in external fertilization. The males and females release their gametes into the water, where they mix and fertilization occurs. Gastropods more often have internal fertilization, however, with the male inserting sperm directly into the female's body. Internal fertilization is one of the key adaptations that allowed gastropods to colonize the land.



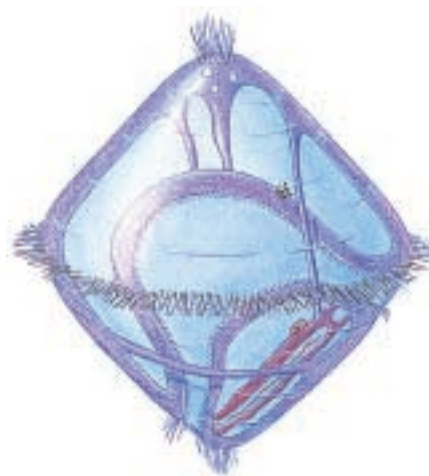
(a)



(b)

**FIGURE 45.6**

**Structure of the radula in a snail.** (a) The radula consists of chitin and is covered with rows of teeth. (b) Enlargement of the rasping teeth on a radula.



(a)



(b)

**FIGURE 45.7**

**Stages in the molluscan life cycle.** (a) The trochophore larva of a mollusk. Similar larvae, as you will see, are characteristic of some annelid worms as well as a few other phyla. (b) Veliger stage of a mollusk.

Many marine mollusks have free-swimming larvae called **trochophores** (figure 45.7a), which closely resemble the larval stage of many marine annelids. Trochophores swim by means of a row of cilia that encircles the middle of their body. In most marine snails and in bivalves, a second free-swimming stage, the veliger, follows the trochophore stage. This **veliger** stage, has the beginnings of a foot, shell, and mantle (figure 45.7b). Trochophores and veligers drift widely in the ocean currents, dispersing mollusks to new areas.

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**Mollusks were among the earliest animals to evolve an efficient excretory system. The mantle of mollusks not only secretes their protective shell, but also forms a cavity that is essential to respiration.**

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## The Classes of Mollusks

There are seven classes of mollusks. We will examine four classes of mollusks as representatives of the phylum: (1) Polyplacophora—chitons; (2) Gastropoda—snails, slugs, limpets, and their relatives; (3) Bivalvia—clams, oysters, scallops, and their relatives; and (4) Cephalopoda—squids, octopuses, cuttlefishes, and nautilus. By studying living mollusks and the fossil record, some scientists have deduced that the ancestral mollusk was probably a dorsoventrally flattened, unsegmented, wormlike animal that glided on its ventral surface. This animal may also have had a chitinous cuticle and overlapping calcareous scales. Other scientists believe that mollusks arose from segmented ancestors and became unsegmented secondarily.

### Class Polyplacophora: The Chitons

Chitons are marine mollusks that have oval bodies with eight overlapping calcareous plates. Underneath the plates, the body is not segmented. Chitons creep along using a broad, flat foot surrounded by a groove or mantle cavity in which the gills are arranged. Most chitons are grazing herbivores that live in shallow marine habitats, but some live at depths of more than 7000 meters.

### Class Gastropoda: The Snails and Slugs

The class Gastropoda contains about 40,000 described species of snails, slugs, and similar animals. This class is primarily a marine group, but it also contains many freshwater and terrestrial mollusks (figure 45.8). Most gastropods have a shell, but some, like slugs and nudibranchs, have lost their shells through the course of evolution. Gastropods generally creep along on a foot, which may be modified for swimming.

The heads of most gastropods have a pair of tentacles with eyes at the ends. These tentacles have been lost in some of the more advanced forms of the class. Within the mouth cavity of many members of this class are horny jaws and a radula.

During embryological development, gastropods undergo **torsion**. Torsion is the process by which the mantle cavity and anus are moved from a posterior location to the front of the body, where the mouth is located. Torsion is brought about by a disproportionate growth of the lateral muscles; that is, one side of the larva grows much more rapidly than the other. A 120-degree rotation of the visceral mass brings the mantle cavity above the head and twists many internal structures. In some groups of gastropods, varying degrees of detorsion have taken place. The **coiling**, or spiral winding, of the shell is a separate process. This process has led to the loss of the right gill and right nephridium in most gastropods. Thus, the visceral mass of gastropods has become bilaterally asymmetrical during the course of evolution.



**FIGURE 45.8**  
A gastropod mollusk. The terrestrial snail, *Allogona townsendiana*.

Gastropods display extremely varied feeding habits. Some are predatory, others scrape algae off rocks (or aquarium glass), and others are scavengers. Many are herbivores, and some terrestrial ones are serious garden and agricultural pests. The radula of oyster drills is used to bore holes in the shells of other mollusks, through which the contents of the prey can be removed. In cone shells, the radula has been modified into a kind of poisonous harpoon, which is shot with great speed into the prey.

Sea slugs, or nudibranchs, are active predators; a few species of nudibranchs have the extraordinary ability to extract the nematocysts from the cnidarian polyps they eat and transfer them through their digestive tract to the surface of their gills intact and use them for their own protection. Nudibranchs are interesting in that they get their name from their gills, which instead of being enclosed within the mantle cavity are exposed along the dorsal surface (*nudi*, “naked”; *branch*; “gill”).

In terrestrial gastropods, the empty mantle cavity, which was occupied by gills in their aquatic ancestors, is extremely rich in blood vessels and serves as a lung, in effect. This structure evolved in animals living in environments with plentiful oxygen; it absorbs oxygen from the air much more effectively than a gill could, but is not as effective under water.

### Class Bivalvia: The Bivalves

Members of the class Bivalvia include the clams, scallops, mussels, and oysters. Bivalves have two lateral (left and right) shells (valves) hinged together dorsally (figure 45.9). A ligament hinges the shells together and causes them to gape open. Pulling against this ligament are one or two large adductor muscles that can draw the shells together.

The mantle secretes the shells and ligament and envelops the internal organs within the pair of shells. The mantle is frequently drawn out to form two siphons, one for an incoming and one for an outgoing stream of water. The siphons often function as snorkels to allow bivalves to filter water through their body while remaining almost completely buried in sediments. A complex folded gill lies on each side of the visceral mass. These gills consist of pairs of filaments that contain many blood vessels. Rhythmic beating of cilia on the gills creates a pattern of water circulation. Most bivalves are sessile filter-feeders. They extract small organisms from the water that passes through their mantle cavity.

Bivalves do not have distinct heads or radulas, differing from gastropods in this respect (see figure 45.5). However, most have a wedge-shaped foot that may be adapted, in different species, for creeping, burrowing, cleansing the animal, or anchoring it in its burrow. Some species of clams can dig into sand or mud very rapidly by means of muscular contractions of their foot.

Bivalves disperse from place to place largely as larvae. While most adults are adapted to a burrowing way of life, some genera of scallops can move swiftly through the water by using their large adductor muscles to clap their shells together. These muscles are what we usually eat as “scallops.” The edge of a scallop’s body is lined with tentacle-like projections tipped with complex eyes.

There are about 10,000 species of bivalves. Most species are marine, although many also live in fresh water. Over 500 species of pearly freshwater mussels, or naiads, occur in the rivers and lakes of North America.

### Class Cephalopoda: The Octopuses, Squids, and Nautilus

The more than 600 species of the class Cephalopoda—octopuses, squids, and nautilus—are the most intelligent of the invertebrates. They are active marine predators that swim, often swiftly, and compete successfully with fish. The foot has evolved into a series of tentacles equipped with suction cups, adhesive structures, or hooks that seize prey efficiently. Squids have 10 tentacles (figure 45.10); octopuses, as indicated by their name, have eight; and the nautilus, about 80 to 90. Once the tentacles have snared the prey, it is bitten with strong, beaklike paired jaws and pulled into the mouth by the tonguelike action of the radula.

Cephalopods have highly developed nervous systems, and their brains are unique among mollusks. Their eyes are very elaborate, and have a structure much like that of vertebrate eyes, although they evolved separately (see chapter 55). Many cephalopods exhibit complex patterns of behavior and a high level of intelligence; octopuses can be easily trained to distinguish among classes of objects. Most members of this class have closed circulatory systems and are the only mollusks that do.



**FIGURE 45.9**  
A bivalve. The file shell, *Lima scabra*, opened, showing tentacles.



**FIGURE 45.10**  
A cephalopod. Squids are active predators, competing effectively with fish for prey.

Although they evolved from shelled ancestors, living cephalopods, except for the few species of nautilus, lack an external shell. Like other mollusks, cephalopods take water into the mantle cavity and expel it through a siphon. Cephalopods have modified this system into a means of jet propulsion. When threatened, they eject water violently and shoot themselves through the water.

Most octopus and squid are capable of changing color to suit their background or display messages to one another. They accomplish this feat through the use of their *chromatophores*, pouches of pigments embedded in the epithelium.

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**Gastropods typically live in a hard shell. Bivalves have hinged shells but do not have a distinct head area. Cephalopods possess well-developed brains and are the most intelligent invertebrates.**

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## 45.2 Annelids were the first segmented animals.

### Segmented Animals

A key transition in the animal body plan was *segmentation*, the building of a body from a series of similar segments. The first segmented animals to evolve were most likely **annelid worms**, phylum Annelida (figure 45.11). One advantage of having a body built from repeated units (segments) is that the development and function of these units can be more precisely controlled, at the level of individual segments or groups of segments. For example, different segments may possess different combinations of organs or perform different functions relating to reproduction, feeding, locomotion, respiration, or excretion.

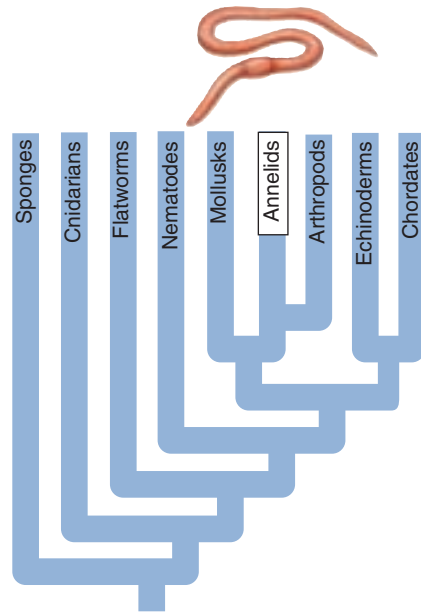


FIGURE 45.11

A **polychaete annelid**. *Nereis virens* is a wide-ranging, predatory, marine polychaete worm equipped with feathery parapodia for movement and respiration, as well as jaws for hunting. You may have purchased *Nereis* as fishing bait!

### Annelids

Two-thirds of all annelids live in the sea (about 8000 species), and most of the rest, some 3100 species, are earthworms. Annelids are characterized by three principal features:

- 1. Repeated segments.** The body of an annelid worm is composed of a series of ring-like segments running the length of the body, looking like a stack of donuts or roll of coins (figure 45.12). Internally, the segments are divided from one another by partitions called **septa**, just as bulkheads separate the segments of a submarine. In each of the cylindrical segments, the excretory and locomotor organs are repeated. The fluid within the coelom of each segment creates a hydrostatic (liquid-supported) skeleton that gives the segment rigidity, like an inflated balloon. Muscles within each segment push against the fluid in the coelom. Because each segment is separate, each can expand or contract independently. This lets the worm move in complex ways.
- 2. Specialized segments.** The anterior (front) segments of annelids have become modified to contain specialized sensory organs. Some are sensitive to light, and elaborate eyes with lenses and retinas have evolved in some annelids. A well-developed cerebral ganglion, or brain, is contained in one anterior segment.
- 3. Connections.** Although partitions separate the segments, materials and information do pass between segments. Annelids have a closed circulatory system that carries blood from one segment to another. A

ventral nerve cord connects the nerve centers or ganglia in each segment with one another and the brain. These neural connections are critical features that allow the worm to function and behave as a unified and coordinated organism.

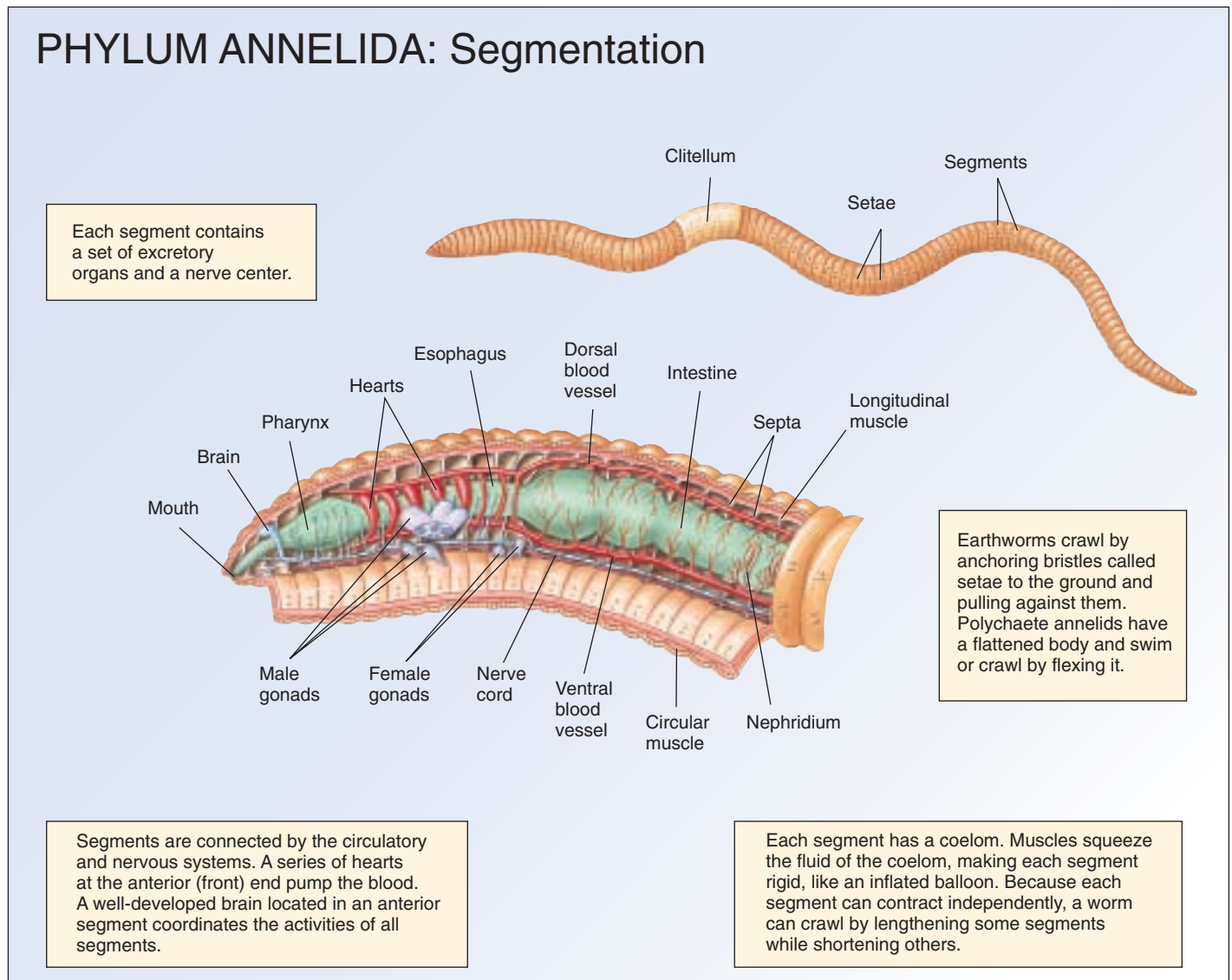
### Body Plan of the Annelids

The basic annelid body plan is a tube within a tube, with the internal digestive tract—a tube running from mouth to anus—suspended within the coelom. The tube that makes up the digestive tract has several portions—the pharynx, esophagus, crop, gizzard, and intestine—that are specialized for different functions.

Annelids make use of their hydrostatic skeleton for locomotion. To move, annelids contract circular muscles running around each segment. Doing so squeezes the segment, causing the coelomic fluid to squirt outwards, like a tube of toothpaste. Because the fluid is trapped in the segment by the septa, instead of escaping like toothpaste, the fluid causes the segment to elongate and get much thinner. By then contracting longitudinal muscles that run along the length of the worm, the segment is returned to its original shape. In most annelid groups, each segment typically possesses **setae**, bristles of chitin that help anchor the worms during locomotion. By extending the setae in some segments so that they anchor in the substrate and retracting them in other segments, the worm can squirt its body, section by section, in either direction.



# PHYLUM ANNELIDA: Segmentation



**FIGURE 45.12**

**The evolution of segmentation.** Marine polychaetes and earthworms (phylum Annelida) were most likely the first organisms to evolve a body plan based on partly repeated body segments. Segments are separated internally from each other by septa.

Unlike the arthropods and most mollusks, most annelids have a closed circulatory system. Annelids exchange oxygen and carbon dioxide with the environment through their body surfaces; most lack gills or lungs. However, much of their oxygen supply reaches the different parts of their bodies through their blood vessels. Some of these vessels at the anterior end of the worm body are enlarged and heavily muscular, serving as hearts that pump the blood. Earthworms have five pulsating blood vessels on each side that serve as hearts, helping to pump blood from the main dorsal vessel, which is their major pumping structure, to the main ventral vessel.

The excretory system of annelids consists of ciliated, funnel-shaped nephridia generally similar to those of mollusks. These nephridia—each segment has a pair—collect waste products and transport them out of the body through the coelom by way of specialized excretory tubes.

**Annelids are a diverse group of coelomate animals characterized by serial segmentation. Each segment in the annelid body has its own circulatory, excretory, neural elements, and setae.**

## Classes of Annelids

The roughly 12,000 described species of annelids occur in many different habitats. They range in length from as little as 0.5 millimeter to the more than 3-meter length of some polychaetes and giant Australian earthworms. There are three classes of annelids: (1) Polychaeta, which are free-living, almost entirely marine bristleworms, comprising some 8000 species; (2) Oligochaeta, terrestrial earthworms and related marine and freshwater worms, with some 3100 species; and (3) Hirudinea, leeches, mainly freshwater predators or bloodsuckers, with about 500 species. The annelids are believed to have evolved in the sea, with polychaetes being the most primitive class. Oligochaetes seem to have evolved from polychaetes, perhaps by way of brackish water to estuaries and then to streams. Leeches share with oligochaetes an organ called a **clitellum**, which secretes a cocoon specialized to receive the eggs. It is generally agreed that leeches evolved from oligochaetes, specializing in their bloodsucking lifestyle as external parasites.

### Class Polychaeta: The Polychaetes

Polychaetes (class Polychaeta) include clamworms, plume worms, scaleworms, lugworms, twin-fan worms, sea mice, peacock worms, and many others. These worms are often surprisingly beautiful, with unusual forms and sometimes iridescent colors (figure 45.13; see also figure 45.1). Polychaetes are often a crucial part of marine food chains, as they are extremely abundant in certain habitats.

Some polychaetes live in tubes or permanent burrows of hardened mud, sand, mucuslike secretions, or calcium carbonate. These sedentary polychaetes are primarily filter feeders, projecting a set of feathery tentacles from the tubes in which they live that sweep the water for food. Other polychaetes are active swimmers, crawlers, or burrowers. Many are active predators.

Polychaetes have a well-developed head with specialized sense organs; they differ from other annelids in this respect. Their bodies are often highly organized into distinct regions formed by groups of segments related in function and structure. Their sense organs include eyes, which range from simple eyespots to quite large and conspicuous stalked eyes.

Another distinctive characteristic of polychaetes is the paired, fleshy, paddlelike flaps, called **parapodia**, on most of their segments. These parapodia, which bear bristlelike setae, are used in swimming, burrowing, or crawling. They also play an important role in gas exchange because they greatly increase the surface area of the body. Some polychaetes that live in burrows or tubes may have parapodia featuring hooks to help anchor the worm. Slow crawling is carried out by means of the parapodia. Rapid crawling and swimming is by undulating the body. In addition, the polychaete epidermis often includes ciliated cells which aid in respiration and food procurement.



**FIGURE 45.13**  
A polychaete. The shiny bristleworm, *Oenone fulgida*.

The sexes of polychaetes are usually separate, and fertilization is often external, occurring in the water and away from both parents. Unlike other annelids, polychaetes usually lack permanent **gonads**, the sex organs that produce gametes. They produce their gametes directly from germ cells in the lining of the coelom or in their septa. Fertilization results in the production of ciliated, mobile *trochophore larvae* similar to the larvae of mollusks. The trochophores develop for long periods in the plankton before beginning to add segments and thus changing to a juvenile form that more closely resembles the adult form.

### Class Oligochaeta: The Earthworms

The body of an earthworm (class Oligochaeta) consists of 100 to 175 similar segments, with a mouth on the first and an anus on the last. Earthworms seem to eat their way through the soil because they suck in organic and other material by expanding their strong pharynx. Everything that they ingest passes through their long, straight digestive tracts. One region of this tract, the gizzard, grinds up the organic material with the help of soil particles.

The material that passes through an earthworm is deposited outside of its burrow in the form of castings that

consist of irregular mounds at the opening of a burrow. In this way, earthworms aerate and enrich the soil. A worm can eat its own weight in soil every day.

In view of the underground lifestyle that earthworms have evolved, it is not surprising that they have no eyes. However, earthworms do have numerous light-, chemo-, and touch-sensitive cells, mostly concentrated in segments near each end of the body—those regions most likely to encounter light or other stimuli. Earthworms have fewer setae than polychaetes and no parapodia or head region.

Earthworms are hermaphroditic, another way in which they differ from most polychaetes. When they mate (figure 45.14), their anterior ends point in opposite directions, and their ventral surfaces touch. The *clitellum* is a thickened band on an earthworm's body; the mucus it secretes holds the worms together during copulation. Sperm cells are released from pores in specialized segments of one partner into the sperm receptacles of the other, the process going in both directions simultaneously.

Two or three days after the worms separate, the clitellum of each worm secretes a mucous cocoon, surrounded by a protective layer of chitin. As this sheath passes over the female pores of the body—a process that takes place as the worm moves—it receives eggs. As it subsequently passes along the body, it incorporates the sperm that were deposited during copulation. Fertilization of the eggs takes place within the cocoon. When the cocoon finally passes over the end of the worm, its ends pinch together. Within the cocoon, the fertilized eggs develop directly into young worms similar to adults.

### Class Hirudinea: The Leeches

Leeches (class Hirudinea) occur mostly in fresh water, although a few are marine and some tropical leeches occupy terrestrial habitats. Most leeches are 2 to 6 centimeters long, but one tropical species reaches up to 30 centimeters. Leeches are usually flattened dorsoventrally, like flatworms. They are hermaphroditic, and develop a clitellum during the breeding season; cross-fertilization is obligatory as they are unable to self-fertilize.

A leech's coelom is reduced and continuous throughout the body, not divided into individual segments as in the polychaetes and oligochaetes. Leeches have evolved suckers at one or both ends of the body. Those that have suckers at both ends move by attaching first one and then the other end to the substrate, looping along. Many species are also capable of swimming. Except for one species, leeches have no setae.

Some leeches have evolved the ability to suck blood from animals. Many freshwater leeches live as external parasites. They remain on their hosts for long periods and suck their blood from time to time.

The best-known leech is the medicinal leech, *Hirudo medicinalis* (figure 45.15). Individuals of *Hirudo* are 10 to 12 centimeters long and have bladelike, chitinous jaws that



**FIGURE 45.14**  
**Earthworms mating.** The anterior ends are pointing in opposite directions.



**FIGURE 45.15**  
*Hirudo medicinalis*, the medicinal leech, is seen here feeding on a human arm. Leeches use chitinous, bladelike jaws to make an incision to access blood and secrete an anticoagulant to keep the blood from clotting. Both the anticoagulant *and* the leech itself have made important contributions to modern medicine.

rasp through the skin of the victim. The leech secretes an anticoagulant into the wound to prevent the blood from clotting as it flows out, and its powerful sucking muscles pump the blood out quickly once the hole has been opened. Leeches were used in medicine for hundreds of years to suck blood out of patients whose diseases were mistakenly believed to be caused by an excess of blood. Today, European pharmaceutical companies still raise and sell leeches, but they are used to remove excess blood after certain surgeries. Following the surgery, blood may accumulate because veins may function improperly and fail to circulate the blood. The accumulating blood “turns off” the arterial supply of fresh blood, and the tissue often dies. When leeches remove the excess blood, new capillaries form in about a week, and the tissues remain healthy.

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**Segmented annelids evolved in the sea. Earthworms are their descendents, as are parasitic leeches.**

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## 45.3 Lophophorates appear to be a transitional group.

### Lophophorates

Three phyla of marine animals—Phoronida, Ectoprocta, and Brachiopoda—are characterized by a **lophophore**, a circular or U-shaped ridge around the mouth bearing one or two rows of ciliated, hollow tentacles. Because of this unusual feature, they are thought to be related to one another. The lophophore presumably arose in a common ancestor. The coelomic cavity of lophophorates extends into the lophophore and its tentacles. The lophophore functions as a surface for gas exchange and as a food-collection organ. Lophophorates use the cilia of their lophophore to capture the organic detritus and plankton on which they feed. Lophophorates are attached to their substrate or move slowly.

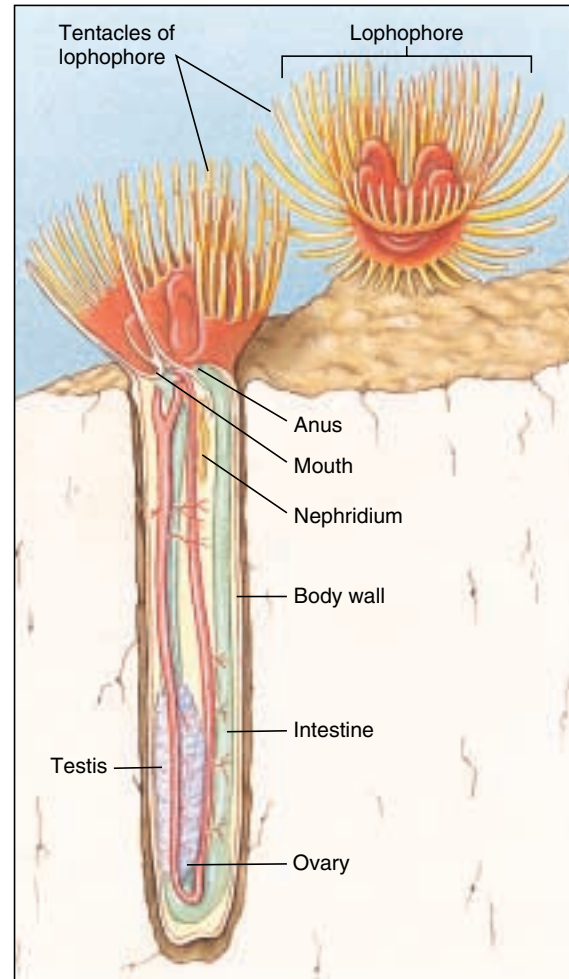
Lophophorates share some features with mollusks, annelids and arthropods (all protostomes) and share others with deuterostomes. Cleavage in lophophorates is mostly radial, as in deuterostomes. The formation of the coelom varies; some lophophorates resemble protostomes in this respect, others deuterostomes. In the Phoronida, the mouth forms from the blastopore, while in the other two phyla, it forms from the end of the embryo opposite the blastopore. Molecular evidence shows that the ribosomes of all lophophorates are decidedly protostome-like, lending strength to placing them within the protostome phyla. Despite the differences among the three phyla, the unique structure of the lophophore seems to indicate that the members share a common ancestor. Their relationships continue to present a fascinating puzzle.

#### Phylum Phoronida: The Phoronids

Phoronids (phylum Phoronida) superficially resemble common polychaete tube worms seen on dock pilings but have many important differences. Each phoronid secretes a chitinous tube and lives out its life within it (figure 45.16). They also extend tentacles to feed and quickly withdraw them when disturbed, but the resemblance to the tube worm ends there. Instead of a straight tube-within-a-tube body plan, phoronids have a U-shaped gut. Only about 10 phoronid species are known, ranging in length from a few millimeters to 30 centimeters. Some species lie buried in sand, others are attached to rocks either singly or in groups. Phoronids develop as protostomes, with radial cleavage and the anus developing secondarily.

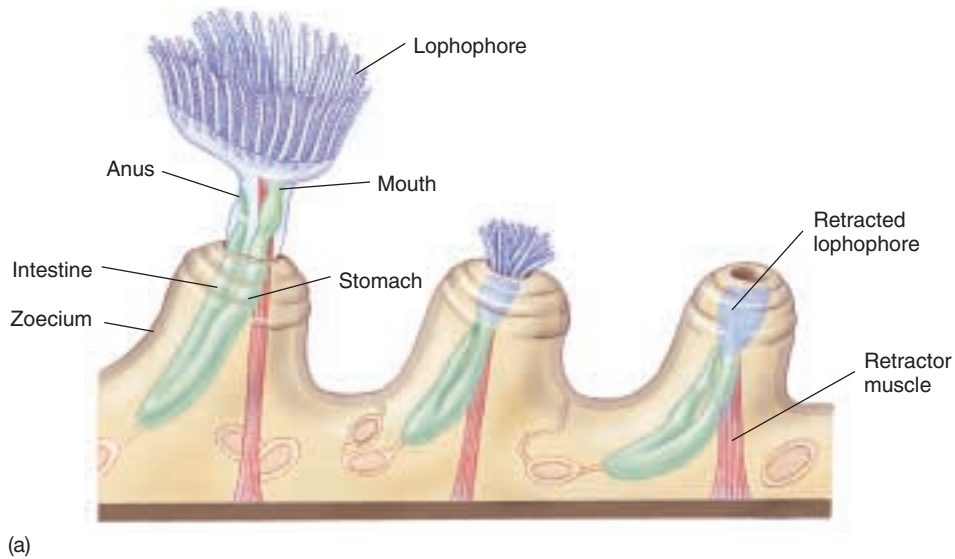
#### Phylum Ectoprocta: The Bryozoans

Ectoprocts (phylum Ectoprocta) look like tiny, short versions of phoronids (figure 45.17). They are small—usually



**FIGURE 45.16**  
**Phoronids (phylum Phoronida).** A phoronid, such as *Phoronis*, lives in a chitinous tube that the animal secretes to form the outer wall of its body. The lophophore consists of two parallel, horseshoe-shaped ridges of tentacles and can be withdrawn into the tube when the animal is disturbed.

less than 0.5 millimeter long—and live in colonies that look like patches of moss on the surfaces of rocks, seaweed, or other submerged objects (in fact, their common name bryozoans translates from Greek as “moss-animals”). The name Ectoprocta refers to the location of the anus (proct), which is external to the lophophore. The 4000 species include both marine and freshwater forms—the only nonmarine lophophorates. Individual ectoprocts secrete a tiny chitinous chamber called a **zoecium** that attaches to rocks and other members of the colony. Individuals communicate chemically through pores between chambers. Ectoprocts develop as deuterostomes, with the mouth developing secondarily; cleavage is radial.

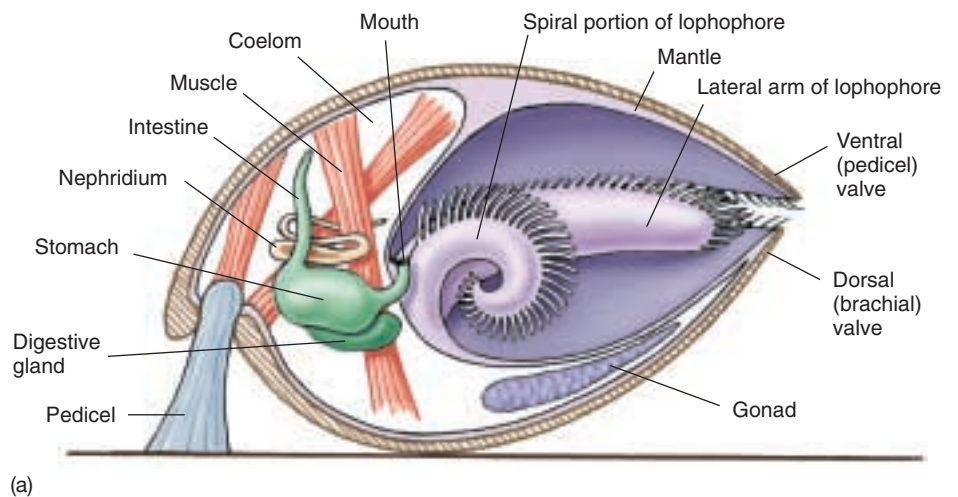


**FIGURE 45.17**  
**Ectoprocts (phylum Ectoprocta).** (a) A small portion of a colony of the freshwater ectoproct, *Plumatella* (phylum Ectoprocta), which grows on the underside of rocks. The individual at the left has a fully extended lophophore, the structure characteristic of the three lophophorate phyla. The tiny individuals of *Plumatella* disappear into their shells when disturbed. (b) *Plumatella repens*, a freshwater bryozoan.

### Phylum Brachiopoda: The Brachiopods

Brachiopods, or lamp shells, superficially resemble clams, with two calcified shells (figure 45.18). Many species attach to rocks or sand by a stalk that protrudes through an opening in one shell. The lophophore lies within the shell and functions when the brachiopod's shells are opened slightly. Although a little more than 300 species of brachiopods (phylum Brachiopoda) exist today, more than 30,000 species of this phylum are known as fossils. Because brachiopods were common in the earth's oceans for millions of years and because their shells fossilize readily, they are often used as index fossils to define a particular time period or sediment type. Brachiopods develop as deuterostomes and show radial cleavage.

The three phyla of lophophorates probably share a common ancestor, and they show a mixture of protostome and deuterostome characteristics.



**FIGURE 45.18**  
**Brachiopods (phylum Brachiopoda).** (a) The lophophore lies within two calcified shells, or valves. (b) The brachiopod, *Terebratulina septentrionalis*, is shown here slightly opened so that the lophophore is visible.

**Summary****Questions****Media Resources****45.1 Mollusks were among the first coelomates.**

- Mollusks contain a true body cavity, or coelom, within the embryonic mesoderm and were among the first coelomate animals.
- The mollusks constitute the second largest phylum of animals in terms of named species. Their body plan consists of distinct parts: a head, a visceral mass, and a foot.
- Of the seven classes of mollusks, the gastropods (snails and slugs), bivalves (clams and scallops), and cephalopods (octopuses, squids, and nautilus), are best known.
- Gastropods typically live in a hard shell. During development, one side of the embryo grows more rapidly than the other, producing a characteristic twisting of the visceral mass.
- Members of the class Bivalvia have two shells hinged together dorsally and a wedge-shaped foot. They lack distinct heads and radulas. Most bivalves are filter-feeders.
- Octopuses and other cephalopods are efficient and often large predators. They possess well-developed brains and are the most intelligent invertebrates.

1. What is the basic body plan of a mollusk? Where is the mantle located? Why is it important in the mollusks? What occurs in the mantle cavity of aquatic mollusks?
2. What is a radula? Do all classes of mollusks possess this structure? How is it used in different types of mollusks?
3. How does the mollusk excretory structure work? Why is it better than the flame cells of acoelomates?
4. What is a trochophore? What is a veliger?
5. Do bivalves generally disperse as larvae or adults? Explain.



• Mollusks

**45.2 Annelids were the first segmented animals.**

- Segmentation is a characteristic seen only in coelomate animals at the annelid evolutionary level and above. Segmentation, or the repetition of body regions, greatly facilitates the development of specialized regions of the body.
- Annelids are worms with bodies composed of numerous similar segments, each with its own circulatory, excretory, and neural elements, and array of setae. There are three classes of annelids, the largely marine Polychaeta, the largely terrestrial Oligochaeta, and the largely freshwater Hirudinea.

6. What evolutionary advantages does segmentation confer upon an organism?
7. What are annelid setae? What function do they serve? What are parapodia? What class of annelids possess them?
8. How do earthworms obtain their nutrients? What sensory structures do earthworms possess? How do these animals reproduce?



• Annelids

• Student Research:  
Growth in  
Earthworms**45.3 Lophophorates appear to be a transitional group.**

- The lophophorates consist of three phyla of marine animals—Phoronida, Ectoprocta, and Brachiopoda—characterized by a circular or U-shaped ridge, the lophophore, around the mouth.
- Some lophophorates have characteristics like protostomes, others like deuterostomes. All are characterized by a lophophore and are thought to share a common ancestor.

9. What prominent feature characterizes the lophophorate animals? What are the functions of this feature?