10

chapter

ten

Molluscs

Fluted giant clam, *Tridacna squamosa*.

A Significant Space

Long ago in the Precambrian era, the most complex animals populating the seas were acoelomate. They must have been inefficient burrowers, and they were unable to exploit the rich subsurface ooze. Any that developed fluid-filled spaces within the body would have had a substantial advantage because these spaces could serve as a hydrostatic skeleton and improve burrowing efficiency.

The simplest, and probably first, mode of achieving a fluid-filled space within the body was retention of the embryonic blastocoel, as in pseudocoelomates. This evolutionary solution was not ideal because organs lay loose in the body cavity. Improved efficiency of a pseudocoel as a hydrostatic skeleton depended on increasingly high hydrostatic pressure, a condition that severely limited the potential for adaptive radiation.

Some descendants of Precambrian acoelomate organisms evolved a more elegant arrangement: a fluid-filled space *within* the mesoderm, the *coelom.* This space was lined with mesoderm, and organs were suspended by mesodermal membranes, the *mesenteries.* Not only could the coelom serve as an efficient hydrostatic skeleton, with circular and longitudinal body-wall muscles acting as antagonists, but a more stable arrangement of organs with less crowding resulted. Mesenteries provided an ideal location for networks of blood vessels, and the alimentary canal could become more muscular, more highly specialized, and more diversified without interfering with other organs.

Development of a coelom was a major step in the evolution of larger and more complex forms. All major groups in chapters to follow are coelomates.

Mollusca (mol-lus´ka) (L. *molluscus,* soft) is one of the largest animal phyla after Arthropoda. There are nearly 50,000 living species and some 35,000 fossil species. The name Mollusca indicates one of their distinctive characteristics, a soft body.

This very diverse group includes organisms as different as chitons, snails, clams, and octopuses (figure 10.1). The group ranges from fairly simple organisms to some of the most complex invertebrates, and in size from almost microscopic to giant squids *Architeuthis harveyi* (Gr. *archi,* primitive, + *teuthis,* squid). The body of this huge species may grow up to 18 m long with tentacles extended. It may weigh up to 454 kg (1000 pounds). The shells of some giant clams *Tridacna gigas* (Gr. *tridaknos,* eaten at three bites) (see figure 10.21), which inhabit the Indo-Pacific coral reefs, reach 1.5 m in length and weigh over 225 kg. These are extremes, however, since probably 80% of all molluscs are less than 5 cm in maximum shell size.

The enormous variety, great beauty, and availability of the shells of molluscs have made shell collecting a popular pastime. However, many amateur shell collectors, although able to name hundreds of the shells that grace our beaches, know very little about the living animals that created those shells and once lived in them. The largest classes of molluscs are Gastropoda (snails and their relatives), Bivalvia (clams, oysters, and others), Polyplacophora (chitons), and Cephalopoda (squids, octopuses, nautiluses). Monoplacophora, Scaphopoda (tusk shells), Caudofoveata, and Solenogastres are much smaller classes.

position in animal kingdom

1. Molluscs are a major group of true **coelomate** animals.
2. They belong to the **protostome** branch, or schizocoelous coelomates, and have spiral cleavage and mosaic development.
3. Many molluscs have a **trochophore larva** similar to the trochophore larva of marine annelids and other marine protostomes. Developmental evidence thus indicates that molluscs and annelids share a common ancestor.
4. Because molluscs are not metameric, they must have diverged from their common ancestor with annelids before the advent of metamerism.
5. All **organ systems** are present and well developed.

biological contributions

1. In molluscs gaseous exchange occurs not only through the body surface as in phyla discussed previously, but also in specialized **respiratory organs** in the form of **gills** or a **lung.**
2. Most classes have an **open circulatory system** with pumping **heart,** vessels, and blood sinuses. In most cephalopods the circulatory system is closed.
3. Efficiency of the respiratory and circulatory systems in cephalopods has made greater body size possible. Invertebrates reach their largest size in some cephalopods.
4. They have a fleshy **mantle** that in most cases secretes a shell and is variously modified for a number of functions. Other features unique to the phylum are the **radula** and the muscular **foot.**
5. The highly developed direct **eye** of cephalopods is similar to the indirect eye of vertebrates but arises as a skin derivative in contrast to the brain eye of vertebrates.

Ecological Relationships

Molluscs are found in a great range of habitats, from tropics to polar seas, at altitudes exceeding 7000 m, in ponds, lakes, and streams, on mudflats, in pounding surf, and in open ocean from the surface to abyssal depths. Most live in the sea, and they represent a variety of lifestyles, including bottom feeders, burrowers, borers, and pelagic forms. The phylum includes some of the most sluggish and some of the swiftest and most active invertebrates. It includes herbivorous grazers, predaceous carnivores, and ciliary filter feeders.

According to fossil evidence, molluscs originated in the sea, and most have remained there. Much of their evolution occurred along shores, where food was abundant and habitats were varied. Only bivalves and gastropods moved on to brackish and freshwater habitats. As filter feeders, bivalves were unable to leave aquatic surroundings; however, snails (gastropods) actually invaded land and may have been the first animals to do so. Terrestrial snails are limited in range by their need for humidity, shelter, and calcium in the soil.

Economic Importance

A group as large as molluscs would naturally affect humans in some way. A wide variety of molluscs are used as food. Pearls, both natural and cultured, are produced in the shells of clams and oysters, most of them in a marine oyster, found around eastern Asia (see figure 10.4B).

Some molluscs are destructive. Burrowing shipworms (see figure 10.24), which are bivalves of several species, do great damage to wooden ships and wharves. To prevent the ravages of shipworms, wharves must be either creosoted or built of concrete. Snails and slugs often damage garden and other vegetation. In addition, many snails serve as intermediate hosts for serious parasites. A certain boring snail, the oyster drill, rivals sea stars in destroying oysters.

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figure 10.1
Molluscs: a diversity of life forms. The basic body plan of this ancient group has become variously adapted for different habitats. **A,** A chiton *(Tonicella lineata)*, class Polyplacophora. **B,** A marine snail *(Calliostoma annulata)*, class Gastropoda. **C,** A nudibranch *(Chromodoris kuniei)*, class Gastropoda. **D,** Pacific giant clam *(Panope abrupta)*, with siphons to the left, class Bivalvia. **E,** An octopus *(Octopus briareus)*, class Cephalopoda, forages at night on a Caribbean coral reef.

Form and Function

Body Plan

Reduced to its simplest dimensions, a mollusc body may be said to consist of a **head-foot** portion and a **visceral mass** portion (figure 10.2). The head-foot is the more active area, containing feeding, cephalic sensory, and locomotor organs. It depends primarily on muscular action for its function. The visceral mass is the portion containing digestive, circulatory, respiratory, and reproductive organs, and it depends primarily on ciliary tracts for its functioning. Two folds of skin, outgrowths of the dorsal body wall, make up a protective **mantle,** which encloses a space between the mantle and body wall called a **mantle cavity.** The mantle cavity houses **gills** or lung, and in some molluscs the mantle secretes a protective **shell** over the visceral mass and head-foot. Modifications of structures that make up the head-foot and the visceral mass produce the great profusion of different patterns seen in this major group of animals.

Head-Foot

Most molluscs have a well-developed head, which bears a mouth and some specialized sensory organs. Photosensory receptors range from fairly simple to the complex eyes of cephalopods. Tentacles are often present. Within the mouth is a structure unique to molluscs, the radula, and usually posterior to the mouth is the chief locomotor organ, or foot.

Radula The radula is a rasping, protrusible, tonguelike organ found in all molluscs except bivalves and some gastropods and solenogasters. It is a ribbonlike membrane on which are mounted rows of tiny teeth that point backward (figure 10.3). Complex muscles move the radula and its supporting cartilages **(odontophore)** in and out while the membrane is partly rotated over the tips of the cartilages. There may be a few or as many as 250,000 teeth, which, when protruded, can scrape, pierce, tear, or cut particles of food material, and the radula may serve as a rasping file for carrying particles in a continuous stream toward the digestive tract.

Foot The molluscan foot may be variously adapted for locomotion, for attachment to a substratum, or for a combination of functions. It is usually a ventral, solelike structure in which waves of muscular contraction effect a creeping locomotion. However, there are many modifications, such as the attachment disc of limpets, the laterally compressed "hatchet foot" of bivalves, or the siphon for jet propulsion in squids and octopuses. Secreted mucus is often used as an aid to adhesion or as a slime track by small molluscs that glide on cilia.

Visceral Mass

Mantle and Mantle Cavity The mantle is a sheath of skin extending from the visceral hump that hangs down on each side of the body, protecting the soft parts and creating between itself and the visceral mass a space called the mantle cavity. The outer surface of the mantle secretes the shell.

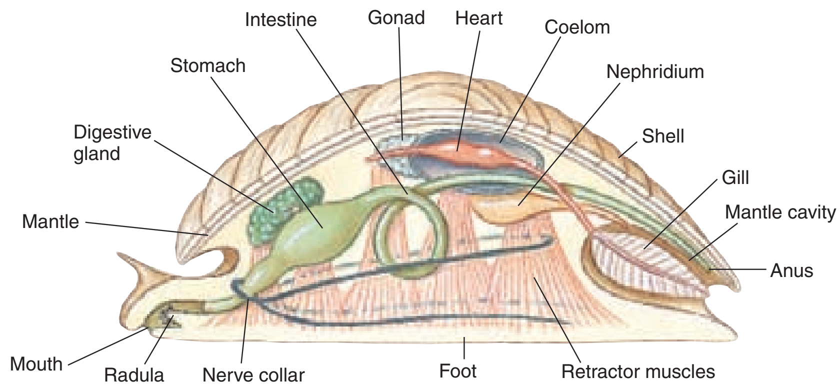


figure 10.2
Generalized mollusc. Although this construct is often presented as a "hypothetical ancestral mollusc" (HAM), most experts now agree that it never actually existed. It is an abstraction used to facilitate description of the general body plan of molluscs.

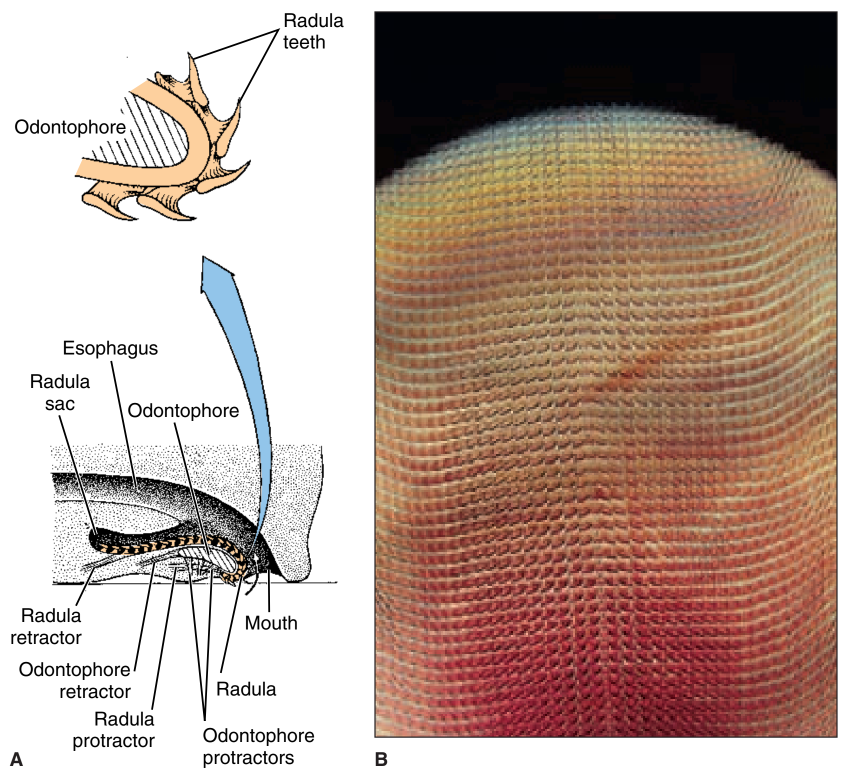


figure 10.3
A, Diagrammatic longitudinal section of gastropod head showing the radula and radula sac. The radula moves back and forth over the odontophore cartilage. As the animal grazes, the mouth opens, the odontophore is thrust forward, the radula gives a strong scrape backward bringing food into the pharynx, and the mouth closes. The sequence is repeated rhythmically. As the radula ribbon wears out anteriorly, it is continually replaced posteriorly. **B,** Radula of a snail prepared for microscopic examination.

The mantle cavity plays an enormous role in the life of a mollusc. It usually houses respiratory organs (gills or lung), which develop from the mantle, and the mantle's own exposed surface serves also for gaseous exchange. Products from the digestive, excretory, and reproductive systems empty into the mantle cavity. In aquatic molluscs a continuous current of water, kept moving by surface cilia or by muscular pumping, brings in oxygen, and in some forms, food; flushes out wastes; and carries reproductive products out to the environment. In aquatic forms the mantle is usually equipped with sensory receptors for sampling the environmental water. In cephalopods (squids and octopuses) the muscular mantle and its cavity create jet propulsion used in locomotion.

Shell The shell of a mollusc, when present, is secreted by the mantle and is lined by it. Typically there are three layers (figure 10.4). The **periostracum** is the outer horny layer, composed of an organic substance called conchiolin, which is a resistant protein. It helps protect the underlying calcareous layers from erosion by boring organisms. It is secreted by a fold of the mantle edge, and growth occurs only at the margin of the shell. On the older parts of the shell the periostracum often becomes worn away. The middle **prismatic layer** is composed of densely packed prisms of calcium carbonate laid down in a protein matrix. It is secreted by the glandular margin of the mantle, and increase in shell size occurs at the shell margin as the animal grows. The inner **nacreous layer** of the

characteristics of phylum mollusca

1. Body bilaterally symmetrical (bilateral asymmetry in some); unsegmented; usually with definite head
2. Ventral body wall specialized as a **muscular foot,** variously modified but used chiefly for locomotion
3. Dorsal body wall forms the **mantle,** which encloses the **mantle cavity,** is modified into **gills** or a **lung,** and secretes the **shell** (shell absent in some)
4. Surface epithelium usually ciliated and bearing mucous glands and sensory nerve endings
5. Coelom mainly limited to area around heart
6. Complex digestive system; rasping organ **(radula)** usually present (see figure 10.3); anus usually emptying into mantle cavity
7. **Open circulatory system** (mostly closed in cephalopods) of heart (usually three chambered, two in most gastropods), blood vessels, and sinuses; respiratory pigments in blood
8. Gaseous exchange by gills, lung, mantle, or body surface
9. Usually one or two kidneys **(metanephridia)** opening into the pericardial cavity and usually emptying into the mantle cavity
10. Nervous system of paired cerebral, pleural, pedal, and visceral ganglia, with nerve cords and subepidermal plexus; ganglia centralized in nerve ring in polyplacophorans, gastropods, and cephalopods
11. Sensory organs of touch, smell, taste, equilibrium, and vision (in some); eyes highly developed in cephalopods

shell is composed of calcium carbonate sheets laid down over a thin protein matrix. This layer is secreted continuously by the mantle surface, so that it becomes thicker during the life of the animal.

Freshwater molluscs usually have a thick periostracum that gives some protection against acids produced in water by decay of leaf litter. In some marine molluscs the periostracum is thick, but in some it is relatively thin or absent. There is a great range in variation in shell structure. Calcium for the shell comes from environmental water or soil or from food. The first shell appears during the larval period and grows continuously throughout life.

Pearl production is a by-product of a protective device used by a mollusc when a foreign object, such as a grain of sand or a parasite, becomes lodged between the shell and mantle. The mantle secretes many layers of nacre around the irritating object (see figure 10.4). Pearls are cultured by inserting small spheres, usually made from pieces of the shells of freshwater clams, in the mantle of a certain species of oyster and by maintaining the oysters in enclosures. The oyster deposits its own nacre around the "seed" in a much shorter time than would be required to form a pearl normally.

Internal Structure and Function

Gaseous exchange occurs through the body surface, particularly the mantle, and in specialized respiratory organs such as gills or lungs. There is an **open circulatory system** with a pumping **heart,** blood vessels, and blood sinuses. Most cephalopods have a closed blood system with heart, vessels, and capillaries. The digestive tract is complex and highly specialized according to feeding habits of the various molluscs.

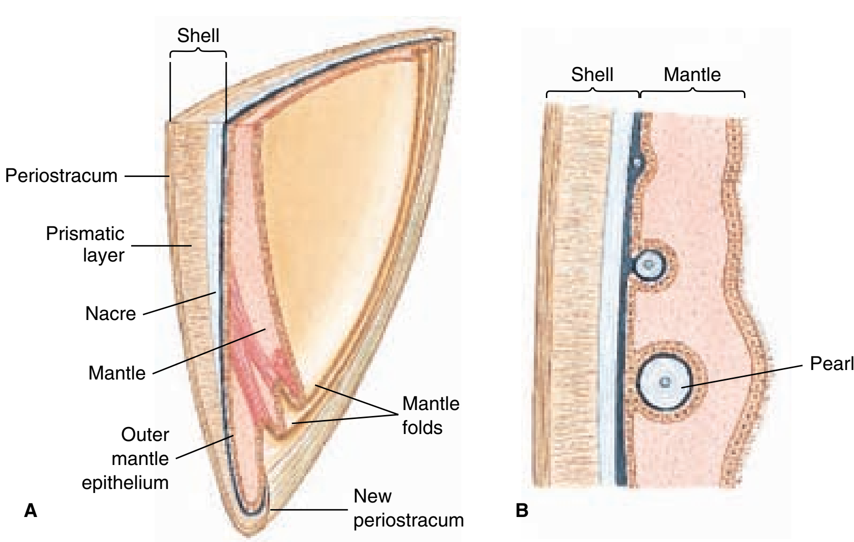


figure 10.4
A, Diagrammatic vertical section of shell and mantle of a bivalve. The outer mantle epithelium secretes the shell; the inner epithelium is usually ciliated. **B,** Formation of pearl between mantle and shell as a parasite or bit of sand under the mantle becomes covered with nacre.

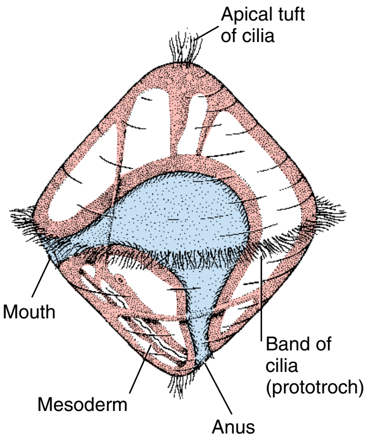


figure 10.5
A generalized trochophore larva. Molluscs and annelids with primitive embryonic development have trochophore larvae, as do several other phyla.

Most molluscs have a pair of **kidneys (metanephridia),** a type of nephridium in which the inner end opens into the coelom; ducts of the kidneys in many forms serve also for discharge of eggs and sperm. The **nervous system** consists of several pairs of ganglia with connecting nerve cords. There are various types of highly specialized sense organs.

Most molluscs are dioecious, although some gastropods are hermaphroditic. Many aquatic molluscs pass through free-swimming **trochophore** (figure 10.5) and **veliger** (figure 10.6) larval stages. A veliger is the free-swimming larva of most marine snails, tusk shells, and bivalves. It develops from a trochophore and has the beginning of a foot, shell, and mantle.

Trochophore larvae (figure 10.5) are minute, translucent, more or less top-shaped, and have a prominent circlet of cilia (prototroch) and sometimes one or two accessory circlets. They are found in molluscs and annelids with primitive embryonic development and considered one of the evidences for common phylogenetic origin of the two phyla. Some form of trochophore-like larva also occurs in marine turbellarians, nemertines, brachiopods, phoronids, sipunculids, and echiurids. Possession of a trochophore or trochophore-like larva supports assignment of these phyla to superphylum Lophotrochozoa.

Classes Caudofoveata and Solenogastres

Caudofoveates and the solenogasters (see figure 10.35, p. 192) are often united in class Aplacophora, and they are both worm-like and shell-less, with calcareous scales or spicules in their

figure 10.6
Veliger of a snail, *Pedicularia,* swimming. The adults are parasitic on corals. The ciliated process (velum) develops from the prototroch of the trochophore (figure 10.5).

integument, with reduced head, and without nephridia. In contrast to caudofoveates, solenogasters usually have no true gills, and they are hermaphroditic. Caudofoveates are burrowing marine animals, feeding on microorganisms and detritus, whereas solenogasters live freely on the ocean bottom and often feed on cnidarians. Caudofoveates may have more features closer to those of ancestral molluscs than do any other living groups.

Class Monoplacophora

Until 1952 Monoplacophora (mon-o-pla-kof´o-ra) were known only from Paleozoic shells. However, in that year living specimens of *Neopilina* (Gr. *neo,* new, + *pilos,* felt cap) were dredged up from the ocean bottom near the west coast of Costa Rica. These molluscs are small and have a low, rounded shell and a creeping foot (figure 10.7). They have a superficial resemblance to limpets, but unlike most other molluscs, a number of organs are serially repeated. Serial repetition occurs to a more limited extent in chitons. Some authors have considered monoplacophorans truly metameric (p. 65), indicating that molluscs descended from a metameric, annelid-like ancestor and that metamerism was lost secondarily in other molluscs. Others believe that *Neopilina* shows only pseudometamerism and that molluscs did not have a metameric ancestor. However, phylogenetic affinity of annelids is strongly supported by embryological and molecular evidence.

Class Polyplacophora: Chitons

Chitons are somewhat flattened and have a convex dorsal surface that bears eight articulating limy **plates,** or **valves,** which give them their name (figures 10.8 and 10.9). The term Polyplacophora means "bearing many plates," in contrast to Monoplacophora, which bear one shell (*mono,* single). The plates

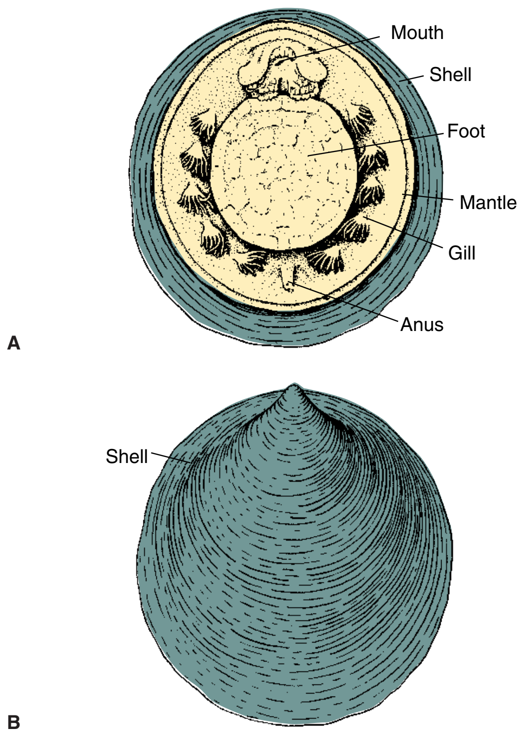


figure 10.7
Neopilina, class Monoplacophora. Living specimens range from 3 mm to about 3 cm in length. **A,** Ventral view. **B,** Dorsal view.

figure 10.8
Mossy chiton, *Mopalia muscosa.* The upper surface of the mantle, or "girdle," is covered with hairs and bristles, an adaptation for defense.

overlap posteriorly and are usually dull colored like the rocks to which chitons cling.

Most chitons are small (2 to 5 cm); the largest rarely exceeds 30 cm. They commonly occur on rocky surfaces in intertidal regions, although some live at great depths. Chitons are stay-at-home organisms, straying only very short distances for feeding. In feeding, a sensory subradular organ protrudes from their mouth to explore for algae or colonial organisms. When some are found, the radula projects to scrape algae off the rocks. A chiton clings tenaciously to its rock with the broad flat foot. If detached, it can roll up like an armadillo for protection.

The mantle forms a **girdle** around the margin of the plates, and in some species mantle folds cover part or all of the plates. On each side of the broad ventral foot and lying between the foot and the mantle is a row of gills suspended from the roof of the mantle cavity. With the foot and the mantle margin adhering

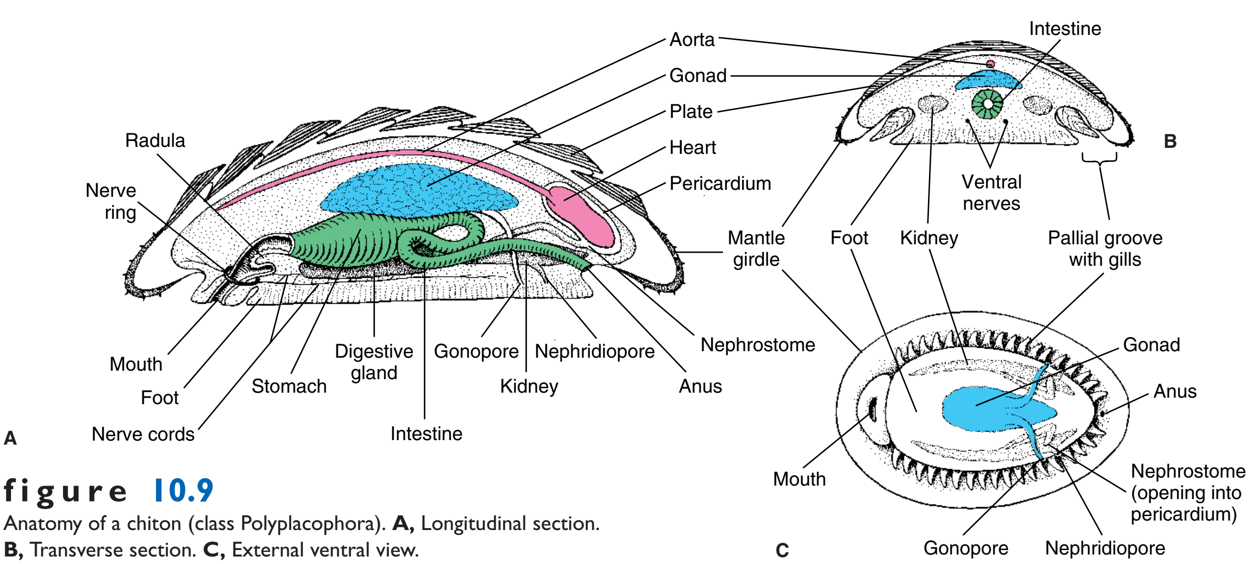


figure 10.9
Anatomy of a chiton (class Polyplacophora). **A,** Longitudinal section. **B,** Transverse section. **C,** External ventral view.

tightly to the substrate, these grooves become closed chambers, open only at the ends. Water enters the grooves anteriorly, flows across the gills, and leaves posteriorly, thus bringing a continuous supply of oxygen to the gills.

Blood pumped by the three-chambered heart reaches the gills by way of an aorta and sinuses. Two kidneys carry waste from the pericardial cavity to the exterior. Two pairs of longitudinal nerve cords are connected in the buccal region. Sense organs include shell eyes on the surface of the shell (in some) and a pair of **osphradia** (chemosensory organs for sampling water).

Sexes are separate in chitons. Sperm shed by males in the excurrent water enter the gill grooves of females by incurrent openings. Eggs are shed into the sea singly or in strings or masses of jelly. Trochophore larvae metamorphose directly into juveniles, without an intervening veliger stage.

Class Scaphopoda

Scaphopoda (ska-fop´o-da), commonly called tusk shells or tooth shells, are sedentary marine molluscs that have a slender body covered with a mantle and a tubular shell open at both ends. Here the molluscan body plan has taken a new direction, with the mantle wrapped around the viscera and fused to form a tube. Most scaphopods are 2.5 to 5 cm long, although they range from 4 mm to 25 cm long.

The foot, which protrudes through the larger end of the shell, functions in burrowing into mud or sand, always leaving the small end of the shell exposed to water above (figure 10.10). Respiratory water circulates through the mantle cavity both by movements of the foot and by ciliary action. Gaseous exchange occurs in the mantle. Most food is detritus and protozoa from the substrate. Cilia of the foot or on the mucus-covered, ciliated knobs of long tentacles catch the food.

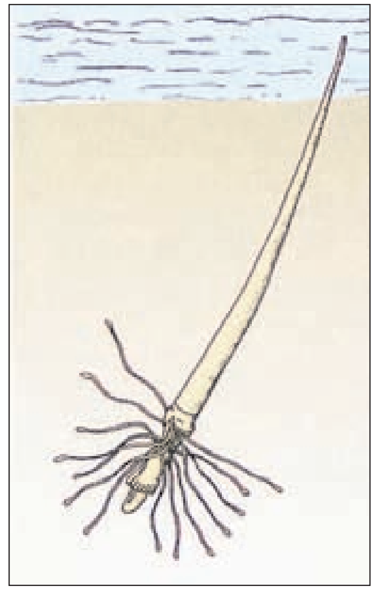


figure 10.10
The tusk shell, *Dentalium,* a scaphopod. It burrows into soft mud or sand and feeds by means of its prehensile tentacles. Respiratory currents of water are drawn in by ciliary action through the small open end of the shell, then expelled through the same opening by muscular action.

Class Gastropoda

Among molluscs class Gastropoda (gas-trop´o-da) (Gr. *gastēr,* stomach, + *pous, podos,* foot) is by far the largest and most diverse, containing about 40,000 living and 15,000 fossil species. Its members differ so widely that there is no single general term in our language that can apply to them as a group. They include snails, limpets, slugs, whelks, conchs, periwinkles, sea slugs, sea hares, sea butterflies, and others. They range from some marine molluscs with many primitive characters to highly evolved, air-breathing snails and slugs.

Gastropods are often sluggish, sedentary animals because most of them have heavy shells and slow locomotor organs. When present, the shell is almost always of one piece (univalve) and may be coiled or uncoiled. Some snails have an **operculum,** a horny plate that covers the shell aperture when the body withdraws into the shell. It protects the body and prevents water loss. These animals are basically bilaterally symmetrical, but because of **torsion,** a twisting process that occurs in the veliger stage, the visceral mass has become asymmetrical.

Form and Function

Torsion

Of all molluscs, only gastropods undergo torsion. Torsion is a peculiar phenomenon that moves the mantle cavity to the front of the body, thus twisting the visceral organs as well through a 90- to 180-degree rotation. Torsion occurs during the veliger stage, and in some species the first part may take only a few minutes. The second 90 degrees typically takes a longer period. Before torsion occurs, the embryo is bilaterally symmetrical with an anterior mouth and a posterior anus and mantle cavity (figure 10.11). The change comes about by an uneven growth of the right and left muscles that attach the shell to the head-foot.

After torsion, the anus and mantle cavity become anterior and open above the mouth and head. The left gill, kidney, and heart auricle are now on the right side, whereas the original right gill, kidney, and heart auricle (lost in most modern gastropods) are now on the left, and the nerve cords have been twisted into a figure eight. Because of the space available in the mantle cavity, the animal's sensitive head end can now be withdrawn into the protection of the shell, with the tougher foot forming a barrier to the outside.

The curious arrangement that results from torsion poses a serious sanitation problem by creating the possibility of wastes being washed back over the gills **(fouling)** and causes us to wonder what evolutionary factors favored such a strange

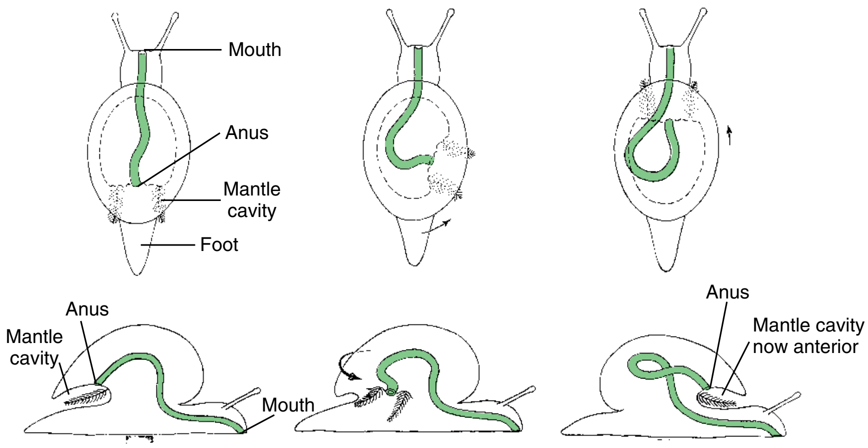


figure 10.11
Torsion in gastropods. **A,** Ancestral condition before torsion. **B,** Intermediate condition. **C,** Early gastropod, torsion complete; direction of crawling now tends to carry waste products back into the mantle cavity, resulting in fouling.

realignment of the body. Several explanations have been proposed, none entirely satisfying. For example, sense organs of the mantle cavity (osphradia) would better sample water when turned in the direction of travel, and as mentioned already, the head could be withdrawn into the shell. Certainly the consequences of torsion and the resulting need to avoid fouling have been very important in the subsequent evolution of gastropods. We cannot explore these consequences, however, until we describe another unusual feature of gastropods—coiling.

Coiling

Coiling, or spiral winding, of the shell and visceral hump is not the same as torsion. Coiling may occur in the larval stage at the same time as torsion, but the fossil record shows that coiling was a separate evolutionary event and originated in gastropods earlier than torsion did. Nevertheless, all living gastropods have descended from coiled, torted ancestors, whether or not they now show these characteristics.

Early gastropods had a bilaterally symmetrical shell with all whorls lying in a single plane (figure 10.12A). Such a shell was not very compact, since each whorl had to lie completely outside the preceding one. Curiously, a few modern species have secondarily returned to that form. The compactness problem of the planospiral shell was solved by a shape in which each succeeding whorl was at the side of the preceding one (figure 10.12B). However, this shape clearly was unbalanced, hanging as it did with much weight over to one side. They achieved better weight distribution by shifting the shell upward and posteriorly, with the shell axis oblique to the longitudinal axis of the foot (figure 10.12C and D). The weight and bulk of the main body whorl, the largest whorl of the shell, pressed on the right side of the mantle cavity, however, and apparently interfered with the organs on that side. Accordingly, the gill, auricle, and kidney of the right side have been lost in all except a few living gastropods, leading to a condition of **bilateral asymmetry.**

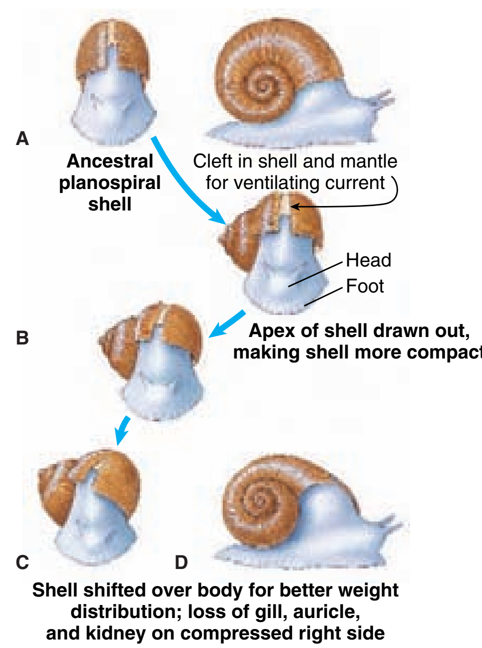


figure 10.12
Evolution of shell in gastropods. **A,** Earliest coiled shells were planospiral, each whorl lying completely outside the preceding whorl. Interestingly, the shell has become planospiral secondarily in some living forms. **B,** Better compactness was achieved by snails in which each whorl lay partially to the side of the preceding whorl. **C** and **D,** Better weight distribution resulted when shell was moved upward and posteriorly.

Adaptations to Avoid Fouling

Although loss of the right gill was probably an adaptation to the mechanics of carrying a coiled shell, that condition made possible a way to avoid fouling, which is displayed in most modern gastropods. Water is brought into the left side of the mantle cavity and out the right side, carrying with it the wastes

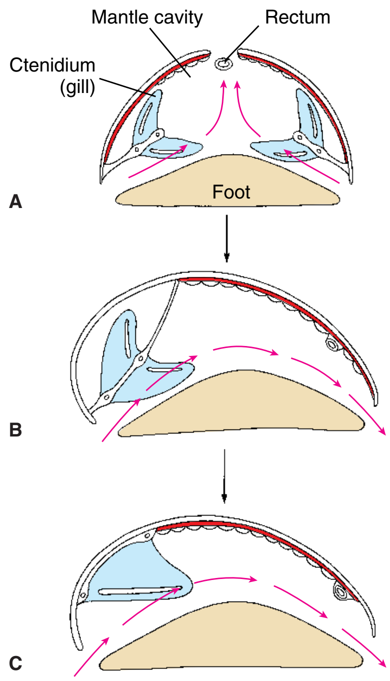


figure 10.13
Evolution of gills in gastropods. **A,** Primitive condition in prosobranchs with two gills and excurrent water leaving the mantle cavity by a dorsal slit or hole. **B,** Condition after one gill had been lost. **C,** Derived condition in prosobranchs, in which filaments on one side of remaining gill are lost, and axis is attached to mantle wall.

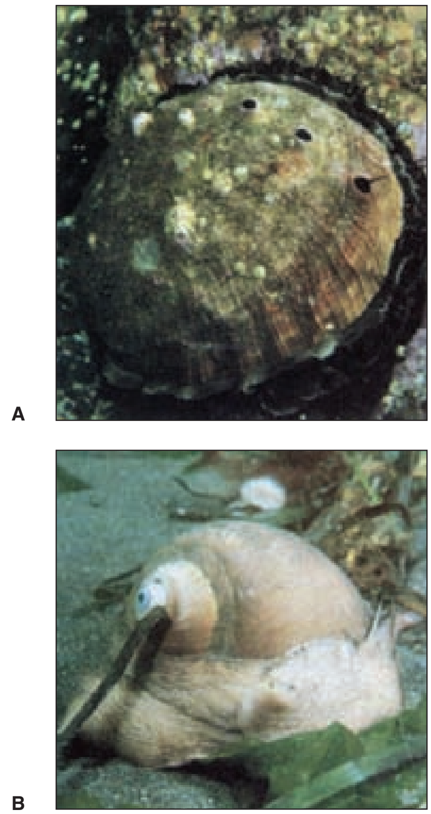


figure 10.14
A, Red abalone, *Haliotus rufescens.* This huge, limpetlike snail is prized as food and extensively marketed. Abalones are strict vegetarians, feeding especially on sea lettuce and kelp. **B,** Moon snail, *Polinices lewisii.* A common inhabitant of West Coast sand flats, the moon snail is a predator of clams and mussels. It uses its radula to drill neat holes through its victim's shell, through which the proboscis is then extended to eat the bivalve's fleshy body.

from the anus and nephridiopore, which lie near the right side (figure 10.13). Some gastropods with primitive characteristics (those with two gills, such as abalone) (figure 10.14A) avoid fouling by venting excurrent water through a dorsal slit or hole in the shell above the anus (see figure 10.12). Opisthobranchs (nudibranchs and others) have evolved an even more curious "twist;" after undergoing torsion as larvae, they develop various degrees of *detorsion* as adults. Pulmonates (most freshwater and terrestrial snails) have lost their gill altogether, and the vascularized mantle wall has become a lung. The anus and nephridiopore open near the opening of the lung to the outside (pneumostome), and waste is expelled forcibly with air or water from the lung.

Feeding Habits

Feeding habits of gastropods are as varied as their shapes and habitats, but all include the use of some adaptation of the radula. Many gastropods are herbivorous, rasping off particles of algae from a substrate. Some herbivores are grazers, some are browsers, some are planktonic feeders. Abalones (figure 10.14) hold seaweed with the foot and break off pieces with their radula. Some snails are scavengers, living on dead and decayed flesh; others are carnivorous, tearing prey apart with their radular teeth. Some, such as oyster borers and moon snails (figure 10.14B), have an extensible proboscis for drilling holes in the shells of bivalves whose soft parts they find delectable. Some even have a spine for opening shells. Most pulmonates (air-breathing snails) (see figure 10.20, p. 183) are herbivorous, but some live on earthworms and other snails.

Some sessile gastropods, such as slipper shells, are ciliary feeders that use the gill cilia to draw in particulate matter, which they roll into a mucous ball and carry to their mouth. Some sea butterflies secrete a mucous net to catch small planktonic forms and then draw the web into their mouth.

After maceration by the radula or by some grinding device, such as the so-called gizzard in sea hares (figure 10.15) and in others, digestion is usually extracellular in the lumen of the stomach or digestive glands. In ciliary feeders the stomachs are sorting regions and most digestion is intracellular in the digestive gland.

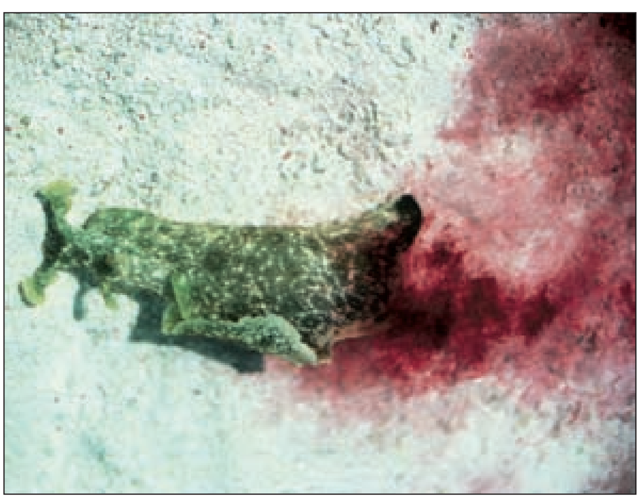
Among the most interesting predators are poisonous cone shells (figure 10.16), which feed on vertebrates or other invertebrates, depending on the species. When *Conus* senses presence of its prey, a single radular tooth slides into position at the tip of the proboscis. When the proboscis strikes prey, it expels the tooth like a harpoon, and the poison tranquilizes or kills the prey at once. Some species can deliver very painful stings, and the sting of several species is lethal to humans. The venom consists of a series of toxic peptides, and each *Conus* species carries peptides **(conotoxins)** specific for the neuroreceptors of its preferred prey.

A

B

figure 10.16
Conus extends its long, wormlike proboscis. When the fish attempts to consume this tasty morsel, the *Conus* stings it in the mouth and kills it. The snail engulfs the fish with its distensible stomach, then regurgitates the scales and bones some hours later.

A



B

figure 10.15
A, Sea hare, *Aplysia dactylomela,* crawls and swims across a coral reef, assisted by large, winglike parapodia, here curled above the body. **B,** When attacked, sea hares squirt a copious protective secretion from their "purple gland" in the mantle cavity.

Internal Form and Function

Respiration in most gastropods is carried out by a gill (two gills in a few), although some aquatic forms lack gills and depend on the skin. The pulmonates have a lung. Freshwater pulmonates must surface to expel a bubble of gas from the lung and curl the edge of the mantle around the **pneumostome** (pulmonary opening in the mantle cavity) (see figure 10.20B) to form a siphon for taking in air.

Most gastropods have a single nephridium (kidney). The circulatory and nervous systems are well developed (figure 10.17). The nervous system includes three pairs of ganglia connected by nerves. Sense organs include eyes, statocysts, tactile organs, and chemoreceptors.

There are both dioecious and hermaphroditic gastropods. During copulation in hermaphroditic species there is sometimes an exchange of **spermatophores** (bundles of sperm), so that self-fertilization is avoided. Many forms perform courtship ceremonies. Most land snails lay their eggs in holes in the ground or under logs. Some aquatic gastropods lay their eggs in gelatinous masses; others enclose them in gelatinous capsules or in parchment egg cases. Most marine gastropods go through a free-swimming veliger larval stage during which torsion and coiling occur. Others develop directly into a juvenile within an egg capsule.

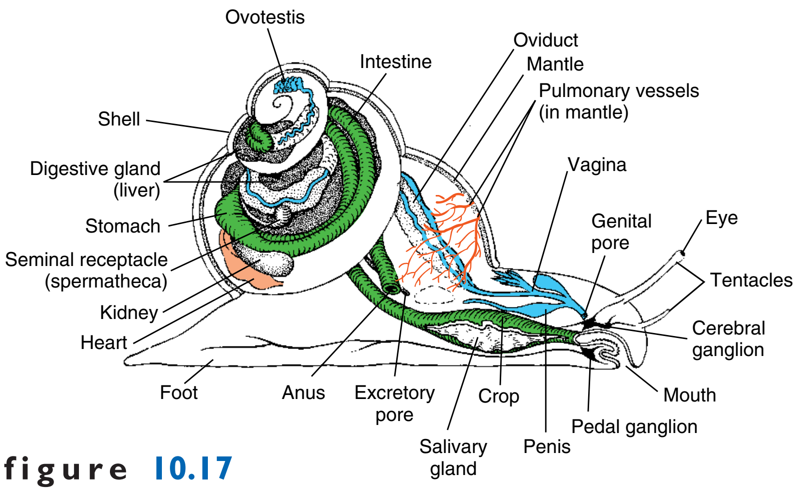


figure 10.17
Anatomy of a pulmonate snail.

Major Groups of Gastropods

Traditional classification of class Gastropoda recognized three subclasses: Prosobranchia, much the largest subclass, almost all of which are marine; Opisthobranchia, an assemblage including sea slugs, sea hares, nudibranchs, and canoe shells—all marine; and Pulmonata, containing most freshwater and terrestrial species. Currently, gastropod taxonomy is in a state of flux, and some workers regard any attempt to present a classification of the class as premature.[1] Nevertheless, present evidence suggests that Prosobranchia is paraphyletic. Opisthobranchia may or may not be paraphyletic, but Opisthobranchia and Pulmonata together apparently form a monophyletic grouping.

Familiar examples of marine gastropods are periwinkles, limpets (figure 10.18A), whelks, conchs, abalones (see figure 10.14A), slipper shells, oyster borers, rock shells, and cowries.

At present 8 to 12 groups of opisthobranchs are recognized. Some have a gill and a shell, although the latter may be vestigial, and some have no shell or true gill. Large sea hares *Aplysia* (see figure 10.15) have large earlike anterior tentacles and a vestigial shell. Nudibranchs have no shell as adults and rank among the most beautiful and colorful of molluscs (figure 10.19). Having lost the gill, the body surface of some nudibranchs is often increased for gaseous exchange by small projections **(cerata),** or a ruffling of the mantle edge.

The third major group (Pulmonata) contains most land and freshwater snails and slugs. Usually lacking gills, their mantle cavity has become a lung, which fills with air by contraction of the mantle floor. Aquatic and a few terrestrial species have one pair of nonretractile tentacles, at the base of which are eyes; land forms usually have two pairs of tentacles, with the posterior pair bearing eyes (figures 10.17 and 10.20). The few nonpulmonate species of gastropods that live in fresh water usually can be distinguished from pulmonates because they have an operculum, which is lacking in pulmonates.

[1]Bieler, R. 1992. Ann. Rev. Ecol. Syst. **23:**311–338.

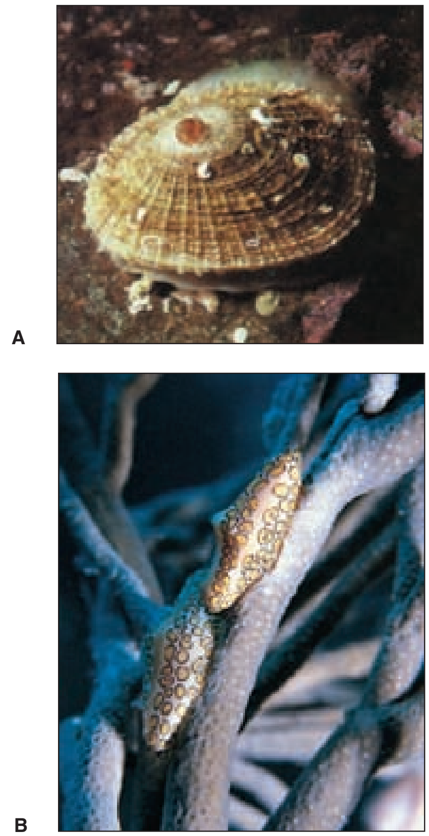


figure 10.18
A, Keyhole limpet, *Diodora aspera,* a prosobranch gastropod with a hole in the apex through which water leaves the mantle cavity. **B,** Flamingo tongues, *Cyphoma gibbosum,* are showy inhabitants of Caribbean coral reefs, where they are associated with gorgonians. These snails have a smooth creamy orange to pink shell that is normally covered by the brightly marked mantle.

figure 10.19
Phyllidia ocellata, a nudibranch. Like other *Phyllidia* spp., it has a hard body with dense calcareous spicules and bears its gills along the sides, between its mantle and foot.

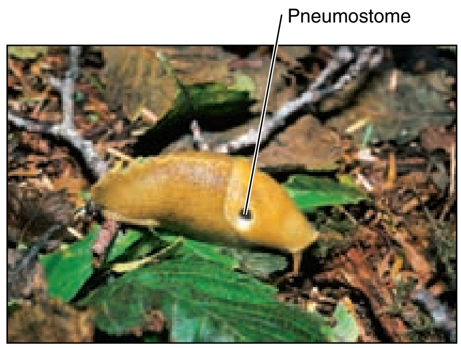


figure 10.20
A, Pulmonate land snail. Note two pairs of tentacles; the second larger pair bears the eyes. **B,** Banana slug, *Ariolimax columbianus*.

Class Bivalvia (Pelecypoda)

Bivalvia (bi-val´ve-a) are also known as Pelecypoda (pel-e-sip´o-da) (Gr. *pelekus,* hatchet, + *pous, podus,* foot). They are bivalved (two-shelled) molluscs that include mussels, clams, scallops, oysters, and shipworms and range in size from tiny seed shells 1 to 2 mm in length to the giant, South Pacific clams *Tridacna,* mentioned previously (figure 10.21). Most bivalves are sedentary **suspension feeders** that depend on ciliary currents produced by the gills to bring in food materials. Unlike gastropods, they have no head, no radula, and very little cephalization (figure 10.22).

Most bivalves are marine, but many live in brackish water and in streams, ponds, and lakes.

Form and Function

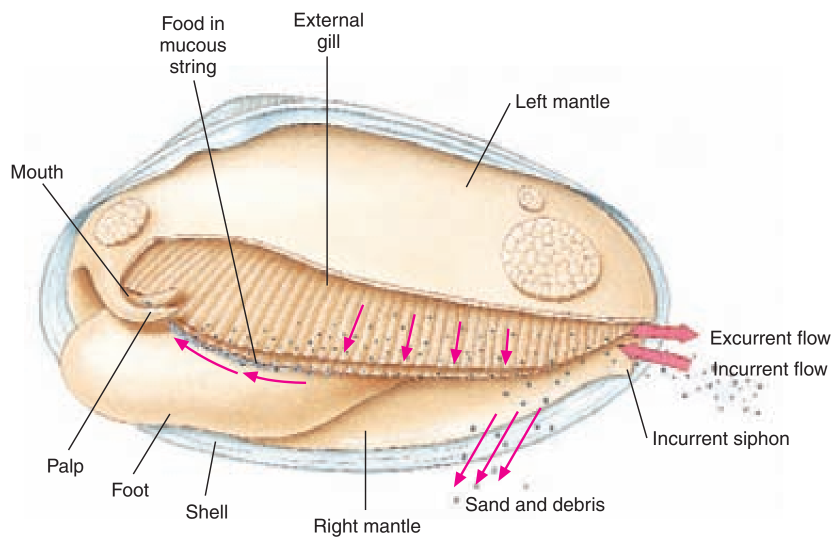
Shell

Bivalves are laterally compressed, and their two shells **(valves)** are held together dorsally by a **hinge ligament** that causes the valves to gape ventrally. **Adductor muscles** work in opposition to the hinge ligament and draw the valves together (figure 10.23C and D). Projecting above the hinge ligament on each valve is the **umbo,** which is the oldest part of the shell. The valves function largely for protection, but those of shipworms (figure 10.24) have microscopic teeth for rasping wood, and rock borers use spiny valves for boring into rock. A few bivalves such as scallops (figure 10.25) use their shells for locomotion by clapping the valves together so that they move in spurts.

Body and Mantle

The **visceral mass** is suspended from the dorsal midline, and the muscular foot is attached to the visceral mass anteroventrally. The gills hang down on each side, each covered by a fold of the mantle. The posterior edges of the mantle folds form dorsal excurrent and ventral incurrent openings (figures 10.23A

figure 10.21
Clam (*Tridacna gigas*) lies buried in coral rock with greatly enlarged siphonal area visible. These tissues are richly colored and bear enormous numbers of symbiotic single-celled algae (zooxanthellae) that provide much of the clam's nutriment.



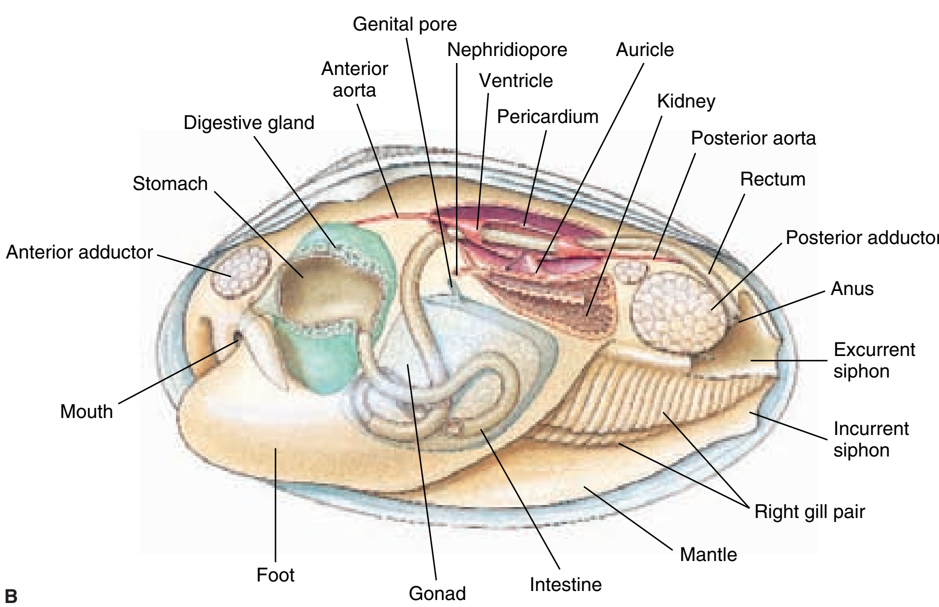


figure 10.22

A, Feeding mechanism of freshwater clam. Left valve and mantle are removed. Water enters the mantle cavity posteriorly and is drawn forward by ciliary action to the gills and palps. As water enters the tiny openings of the gills, food particles are sieved out and caught up in strings of mucus that are carried by cilia to the palps and directed to the mouth. Sand and debris drop into the mantle cavity and are removed by cilia. **B,** Clam anatomy.

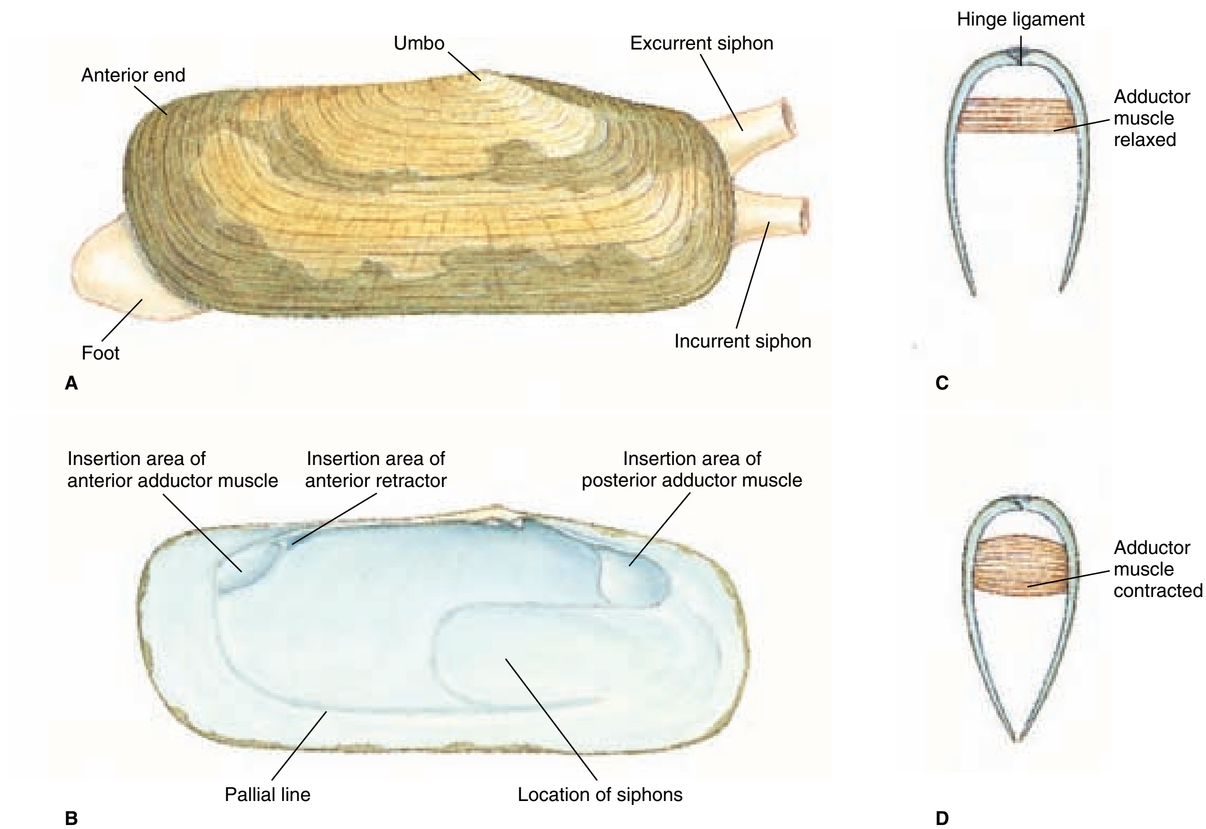


figure 10.23

Tagelus plebius, the stubby razor clam (class Bivalvia). **A,** External view of left valve. **B,** Inside of right shell showing scars where muscles were attached. The mantle was attached to the pallial line. **C** and **D,** Sections showing function of adductor muscles and hinge ligament. In **C** the adductor muscle is relaxed, allowing the hinge ligament to pull the valves apart. In **D** the adductor muscle is contracted, pulling the valves together.

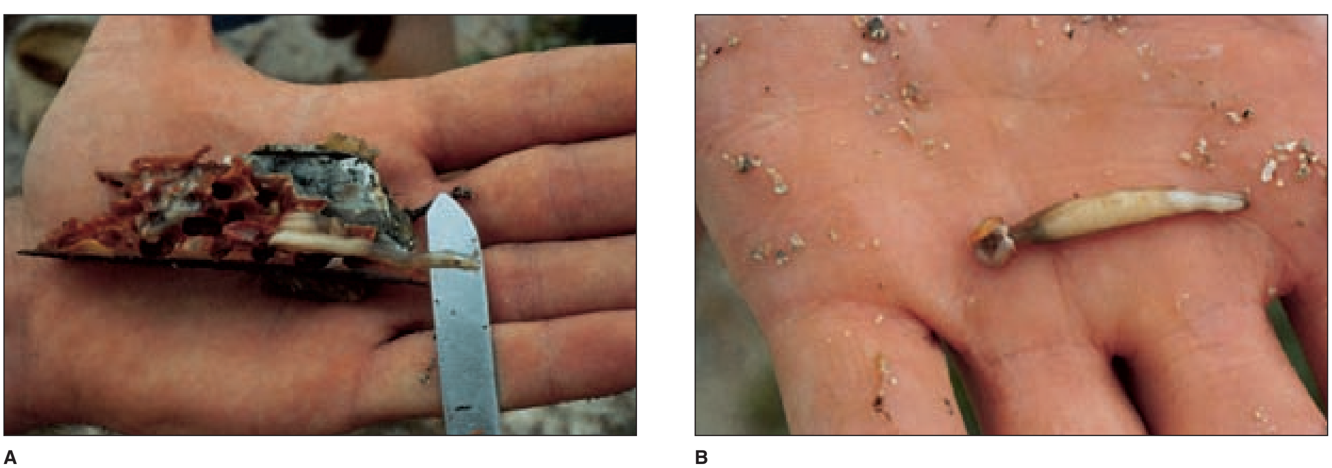


figure 10.24

A, Shipworms (*Teredo, Bankia,* and others) are bivalves that burrow in wood, causing great damage to unprotected wooden hulls and piers. **B,** The two small, anterior valves, seen at left, are used as rasping organs to extend the burrow.

figure 10.25
Representing a group that has evolved from burrowing ancestors, the surface-dwelling bay scallop *Aequipecten irradians* has developed sensory tentacles and a series of blue eyes along its mantle edges.

figure 10.26
In northwest ugly clams, *Entodesma navicula,* the incurrent and excurrent siphons are clearly visible.

and 10.26). In some marine bivalves part of the mantle is drawn out into long muscular siphons to allow the clam to burrow into the mud or sand and extend the siphons to the water above. Cilia on the gills and inner surface of the mantle direct the flow of water over the gills.

Locomotion

Most bivalves move by extending their slender muscular foot between the valves (see figure 10.23A). They pump blood into the foot, causing it to swell and to act as an anchor in mud or sand, then longitudinal muscles contract to shorten the foot and pull the animal forward. In most bivalves the foot is used for burrowing, but a few creep. Some bivalves are sessile: oysters attach their shells to a surface by secreting cement, and mussels (figure 10.27) attach themselves by secreting a number of slender **byssal threads.**

figure 10.27
Mussels, *Mytilus edulis,* occur in northern oceans around the world; they form dense beds in the intertidal zone. A host of marine creatures live protected beneath attached mussels.

Feeding and Digestion

Most bivalves are suspension feeders. Their respiratory currents bring both oxygen and organic materials to their gills where ciliary tracts direct them to the tiny pores of the gills. Gland cells on the gills and labial palps secrete copious amounts of mucus, which entangles particles suspended in the water going through gill pores. Ciliary tracts move the particle-laden mucus to the mouth (see figure 10.22).

In the stomach the mucus and food particles are kept whirling by a rotating gelatinous rod, called a **crystalline style.** Solution of layers of the rotating style frees digestive enzymes for extracellular digestion. Ciliated ridges of the stomach sort food particles and direct suitable particles to the **digestive gland** for intracellular digestion.

Shipworms (see figure 10.24) feed on the particles they excavate as they burrow in wood. Symbiotic bacteria live in a special organ in these bivalves and produce cellulase to digest wood. Other bivalves such as giant clams gain much of their nutrition from the photosynthetic products of symbiotic algae (zooxanthellae, p. 98) living in their mantle tissue (see figure 10.21).

Internal Features and Reproduction

Bivalves have a three-chambered heart that pumps blood through the gills and mantle for oxygenation and to the kidneys for waste elimination (figure 10.28). They have three pairs of widely separated ganglia and poorly developed sense organs. A few bivalves have ocelli. The steely blue eyes of some scallops (see figure 10.25), located around the mantle edge, are remarkably complex, equipped with cornea, lens, and retina.

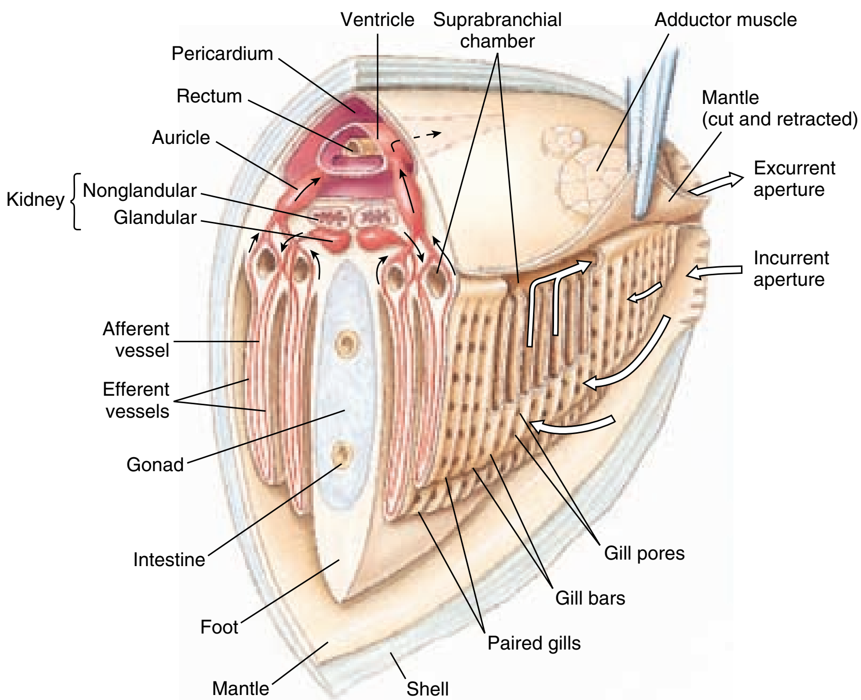
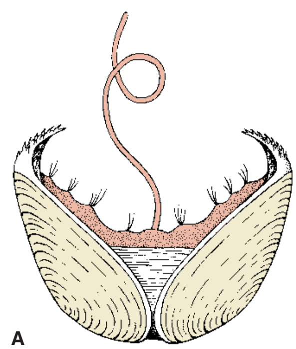


figure 10.28
Section through heart region of a freshwater clam to show relation of circulatory and respiratory systems. Respiratory water currents: water is drawn in by cilia, enters gill pores, and then passes up water tubes to suprabranchial chambers and out excurrent aperture. Blood in gills exchanges carbon dioxide and oxygen. Blood circulation: ventricle pumps blood forward to sinuses of foot and viscera, and posteriorly to mantle sinuses. Blood returns from mantle to auricles; it returns from viscera to the kidney, and then goes to the gills, and finally to the auricles.

Sexes are separate, and fertilization is usually external. Marine embryos typically go through three free-swimming larval stages—**trochophore, veliger larva,** and young **spat**—before reaching adulthood. In freshwater clams fertilization is internal, and some gill tubes become temporary brood chambers. There larvae develop into specialized veligers called **glochidia,** which are discharged with the excurrent flow (figure 10.29). If glochidia come in contact with a passing fish, they hitchhike a ride as parasites in the fish's gills for the next 20 to 70 days before sinking to the bottom to become sedentary adults.

> Freshwater clams were once abundant and diverse in streams throughout the eastern United States, but they are now easily the most jeopardized group of animals in the country. Of the more than 300 species once present, 12 are extinct, 42 are listed as threatened or endangered, and as many as 88 more may be listed soon. A combination of causes is responsible, of which a decline in water quality is among the most important. Pollution and sedimentation from mining, industry, and agriculture are among the culprits. Habitat destruction by altering natural water courses and damming is an important factor. Poaching to supply the Japanese cultured pearl industry is partially to blame (see note on p. 175). And in addition to everything else, the prolific zebra mussels (see next note) attach in great numbers to native clams, exhausting food supplies (phytoplankton) in the surrounding water.



A

B

figure 10.29
A, Glochidium, or larval form, for some freshwater clams. When larvae are released from brood pouch of mother, they may become attached to a fish's gill by clamping their valves closed. They remain as parasites on the fish for several weeks. Their size is approximately 0.3 mm.
B, Some clams have adaptations that help their glochidia find a host. The mantle edge of this female pocketbook mussel (*Lampsilis ovata*) mimics a small minnow, complete with eye. When a smallmouth bass comes to dine, it gets doused with glochidia.

Zebra mussels, *Dreissena polymorpha,* are a recent and potentially disastrous biological introduction into North America. They were apparently picked up as veligers with ballast water by one or more ships in freshwater ports in northern Europe and then expelled between Lake Huron and Lake Erie in 1986. This 4 cm bivalve spread throughout the Great Lakes by 1990, and by 1994 it was as far south on the Mississippi as New Orleans, as far north as Duluth, Minnesota, and as far east as the Hudson River in New York. It attaches to any firm surface and filter feeds on phytoplankton. Large numbers build up rapidly. They foul water intake pipes of municipal and industrial plants, impede intake of water for municipal supplies, and have far-reaching effects on the ecosystem (see preceding note). Zebra mussels will cost billions of dollars to control.

Class Cephalopoda

Cephalopoda (sef-a-lop´o-da) are the most complex of the molluscs—in fact, in some respects they are the most complex of all invertebrates. They include squids, octopuses, nautiluses, and cuttlefishes. All are marine, and all are active predators.

Cephalopods (Gr. *kephalē,* head, + *pous, podos,* foot) have a modified foot that is concentrated in the head region. It takes the form of a funnel for expelling water from the mantle cavity, and the anterior margin is drawn out into a circle or crown of arms or tentacles.

Cephalopods range in size from 2 to 3 cm up to the giant squid, *Architeuthis,* which is the largest invertebrate known. The squid *Loligo* (L., cuttlefish) is about 30 cm long (figure 10.30A).

The enormous giant squid, *Architeuthis,* is very poorly known because no one has ever been able to study a living specimen. The anatomy has been studied from stranded animals, from those captured in nets of fishermen, and from specimens found in stomachs of sperm whales. The mantle length is 5 to 6 m, and the head is up to one meter long. They have the largest eyes in the animal kingdom: up to 25 cm (10 inches) in diameter. They apparently eat fish and other squids, and they are an important food item for sperm whales. They are thought to live on or near the ocean bottom at a depth of 1000 m, but some have been seen swimming at the surface.

Fossil records of cephalopods go back to Cambrian times. The earliest shells were straight cones; others were curved or coiled, culminating in a coiled shell similar to that of the modern *Nautilus* spp. (Gr. *nautilos,* sailor)—the only remaining members of the once flourishing nautiloids (figure 10.31). Cephalopods without shells or with internal shells (such as octopuses and squids) probably evolved from a straight-shelled ancestor. Ammonoids were widely prevalent in the Mesozoic era but became extinct by the end of the Cretaceous period. They had chambered shells analogous to nautiloids, but the septa were more complex. Reasons for their extinction remain a mystery. Present evidence suggests that they were gone before the asteroid bombardment at the end of the Cretaceous period (p. 29), and some nautiloids, which some ammonoids closely resembled, survive to the present.

Form and Function

Shell

Although early nautiloid and ammonoid shells were heavy, they were made buoyant by a series of **gas chambers,** as is that of *Nautilus* (figure 10.31B), enabling the animal to swim while carrying its shell. The shell of *Nautilus,* although coiled, is quite different from that of a gastropod. Transverse septa divide the shell into internal chambers (figure 10.31B). The living animal inhabits only the last chamber. As it grows, it moves forward, secreting behind it a new septum. The chambers are connected by a cord of living tissue called a **siphuncle,** which extends from the visceral mass. Cuttlefishes also have a small coiled or curved shell, but it is entirely enclosed by the mantle. In squids most of the shell has disappeared, leaving only a thin, horny strip called a **pen,** which the mantle encloses. In *Octopus* (Gr. *oktos,* eight, + *pous, podos,* foot) the shell is absent.

After *Nautilus* secretes a new septum, the new chamber is filled with fluid similar in ionic composition to that of the *Nautilus'* blood (and of seawater). Fluid removal involves the active secretion of ions into tiny intercellular spaces in the siphuncular epithelium, so that a very high local osmotic pressure is produced, and the water is drawn out of the chamber by osmosis. The gas in the chamber is only the respiratory gas from the siphuncle tissue that diffuses into the chamber as the fluid is removed. Thus the gas pressure in the chamber is 1 atmosphere or less because it is in equilibrium with the gases dissolved in the seawater surrounding the *Nautilus,* which are in turn in equilibrium with air at the surface of the sea, despite the fact that the *Nautilus* may be swimming at 400 m beneath the surface. That the shell can withstand implosion by the surrounding 41 atmospheres (about 600 pounds per square inch), and that the siphuncle can remove water against this pressure are marvelous feats of natural engineering!

Locomotion

Most cephalopods swim by forcefully expelling water from the mantle cavity through a ventral **funnel**—a sort of jet-propulsion method. The funnel is mobile and can be pointed forward or backward to control direction; the force of water expulsion determines speed.

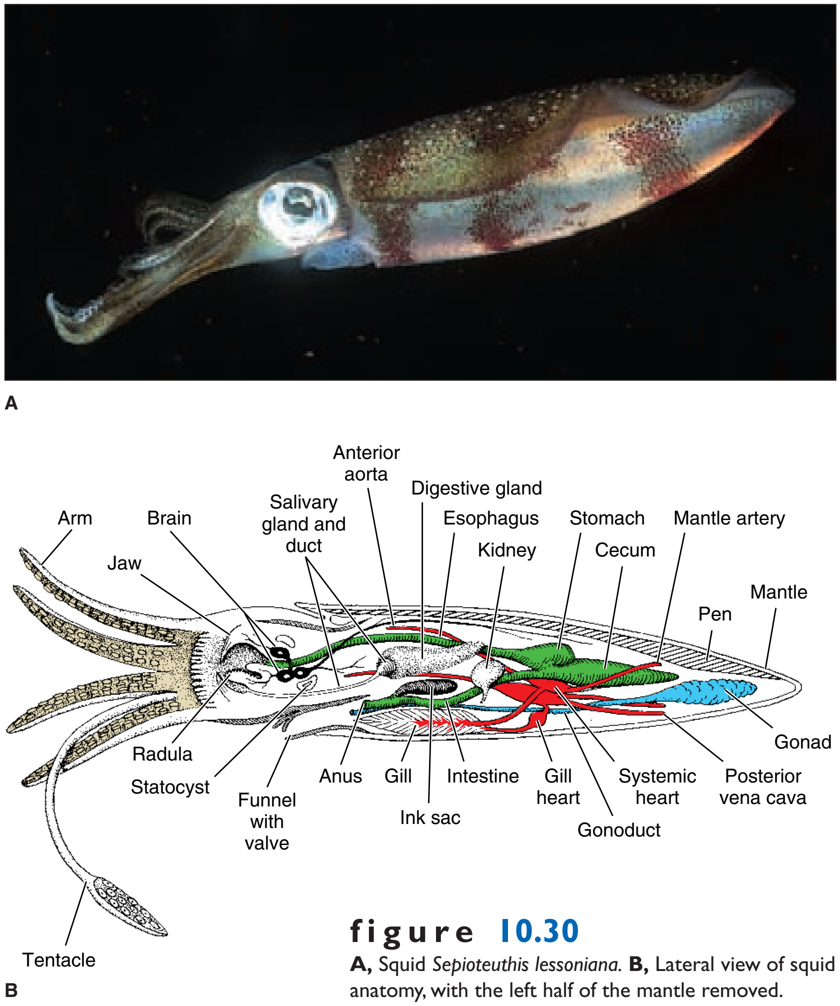


figure 10.30
A, Squid *Sepioteuthis lessoniana.* **B,** Lateral view of squid anatomy, with the left half of the mantle removed.

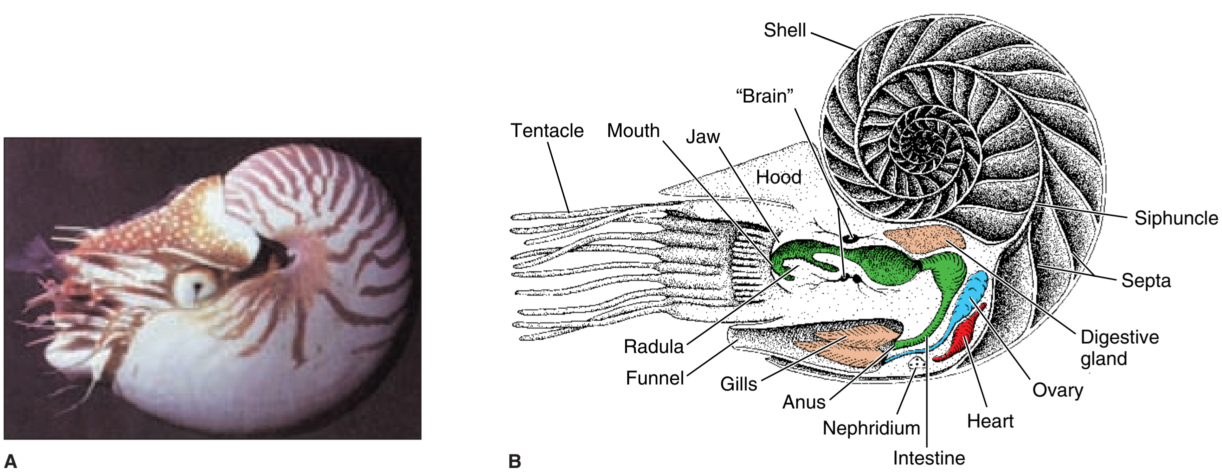


figure 10.31
Nautilus, a cephalopod. **A,** Live *Nautilus,* feeding on a fish. **B,** Longitudinal section, showing gas-filled chambers of shell, and diagram of body structure.

figure 10.32
Cuttlefish, *Sepia latimanus,* has an internal shell familiar to keepers of caged birds as "cuttlebone."

Squids and cuttlefishes are excellent swimmers. The squid body is streamlined and built for speed (figure 10.30). Cuttlefishes swim more slowly (figure 10.32). Both squids and cuttlefishes have lateral fins that can serve as stabilizers, but they are held close to the body for rapid swimming. The gas-filled chambers of *Nautilus* keep the shell upright. Although not as fast as squids, they move surprisingly well.

Octopus has a rather globular body and no fins (see figure 10.1E). Octopuses can swim backwards by spurting jets of water from their funnel, but they are better adapted to crawling about over the rocks and coral, using the suction discs on their arms to pull or to anchor themselves. Some deep-water octopods have fins and arms webbed like an umbrella; they swim in a medusa-like fashion.

External Features

During embryonic development of cephalopods, the head and foot become indistinguishable. The ring around the mouth, which bears the arms and tentacles, is apparently derived from the anterior margin of the head.

In *Nautilus* the head with its 60 to 90 or more tentacles can be extruded from the opening of the body compartment of the shell (see figure 10.31). Its tentacles have no suckers but adhere to prey by secretions. The tentacles search for, sense, and grasp food. Beneath the head is the funnel. The shell shelters the mantle, mantle cavity, and visceral mass. Two pairs of gills are located in the mantle cavity.

Cephalopods other than nautiloids have only one pair of gills. Octopods have 8 arms with suckers; squids and cuttlefishes (decapods) have 10 arms: 8 arms with suckers and a pair of long retractile tentacles. The thick mantle covering the trunk fits loosely at the neck region allowing intake of water into the mantle cavity. When the mantle edges contract closely about the neck, water is expelled through the funnel. The water current thus created provides oxygenation for the gills in the mantle cavity, jet power for locomotion, and a means of carrying wastes and sexual products away from the body.

Color Changes

There are special pigment cells called **chromatophores** in the skin of most cephalopods, which by expanding and contracting produce color changes. They are controlled by the nervous system and perhaps by hormones. Some color changes are protective to match background hues; most are behavioral and are associated with alarm or courtship. Many deep-sea squids are bioluminescent.

Ink Production

Most cephalopods other than nautiloids have an ink sac that empties into the rectum. The sac contains an ink gland that secretes a dark fluid containing the pigment melanin. When the animal is alarmed, it releases a cloud of ink through the anus to form a "smokescreen" to confuse an enemy.

Feeding and Nutrition

Cephalopods are predaceous, feeding chiefly on small fishes, molluscs, crustaceans, and worms. Their arms, which are used in food capture and handling, have a complex musculature and are capable of delicately controlled movements. They are highly mobile and swiftly seize prey and bring it to the mouth. Strong, beaklike **jaws** grasp prey, and the **radula** tears off pieces of flesh (see figure 10.30B). Octopods and cuttlefishes have salivary glands that secrete a poison for immobilizing prey. Digestion is extracellular and occurs in the stomach and cecum.

Internal Features and Reproduction

The active habits of cephalopods are reflected in their internal anatomy, particularly their respiratory, circulatory, and nervous systems. They have the most complex brain among invertebrates (see figure 10.30B). Except for *Nautilus,* which has relatively simple eyes, cephalopods have elaborate eyes with cornea, lens, chambers, and retina (figure 10.33)—similar to the camera-type eye of vertebrates.

Ciliary propulsion would not circulate enough water over the gills for an active animal, and cephalopods ventilate their gills by muscular action of the mantle wall. They have a closed circulatory system with a network of vessels, and blood flows through the gills via capillaries. The plan of circulation of the ancestral mollusc places the entire systemic circulation before blood reaches the gills, which means that the blood pressure at the gills is too low for rapid gaseous exchange. This functional problem has been solved by the evolution of **accessory** or **branchial (gill) hearts** (see figure 10.30B).

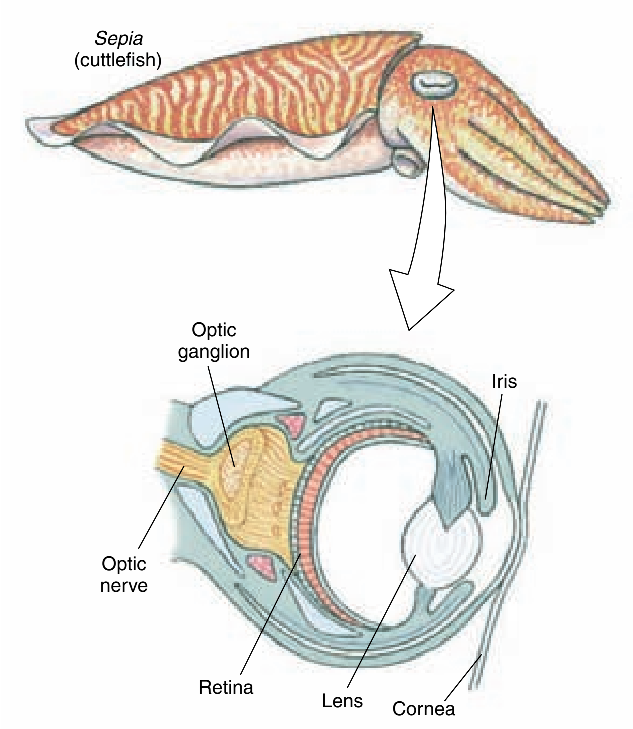


figure 10.33
Eye of a cuttlefish (*Sepia*). The structure of cephalopod eyes shows a high degree of convergent evolution with eyes of vertebrates.

Sexes are separate in cephalopods. In the male seminal vesicle spermatozoa are encased in spermatophores and stored in a sac that opens into the mantle cavity. During copulation one arm of an adult male plucks a spermatophore from his own mantle cavity and inserts it into the mantle cavity of a female near the oviduct opening (figure 10.34). Before copulation males often undergo color displays, apparently directed against rival males and for courtship of females. Eggs are fertilized as they leave the oviduct and are usually attached to stones or other objects to develop. Some octopods tend their eggs.

Phylogeny and Adaptive Radiation

The first molluscs probably arose during Precambrian times because fossils attributed to Mollusca have been found in geological strata as old as the early Cambrian period. On the basis of such shared features as spiral cleavage, mesoderm from the 4d blastomere, and trochophore larva, most zoologists have accepted Mollusca as protostomes, allied with annelids and arthropods. Opinions differ, however, as to whether molluscs were derived from a flatwormlike ancestor independent of annelids, share an ancestor with annelids after the advent of the coelom, or share a metameric common ancestor with annelids. This last hypothesis is strengthened if *Neopilina* (class Monoplacophora) can be considered metameric, as some scientists have contended. However, it is unlikely that such a successful adaptation as metamerism would have been lost in all later molluscs, and there is no trace of metamerism in development of any known molluscan larva. Therefore most zoologists now suggest that the replication of body parts found in the monoplacophorans is pseudometamerism. The most reasonable hypothesis is that molluscs branched from the annelid line after the coelom arose but before the advent of metamerism. Some analyses suggest that molluscs and annelids are more closely related to each other than either is to arthropods. This contention is strengthened by molecular evidence that places annelids and molluscs in Lophotrochozoa and arthropods in Ecdysozoa (p. 81). The Lophotrochozoa/Ecdysozoa hypothesis, however, requires that metamerism arose at least twice independently.

A "hypothetical ancestral mollusc" (see figure 10.2) was long viewed as representing the original mollusc ancestor, but neither a solid shell nor a broad, crawling foot are now considered universal characters for Mollusca. The primitive ancestral mollusc was probably a more or less wormlike organism with a ventral gliding surface and a dorsal mantle with a chitinous cuticle and calcareous scales (figure 10.35). It had a posterior mantle cavity with two gills, a radula, a ladderlike nervous system, and an open circulatory system with a heart. Among living molluscs the primitive condition is most nearly approached by caudofoveates, although the foot is reduced to an oral shield in members of this class. Solenogasters have lost the gills, and the

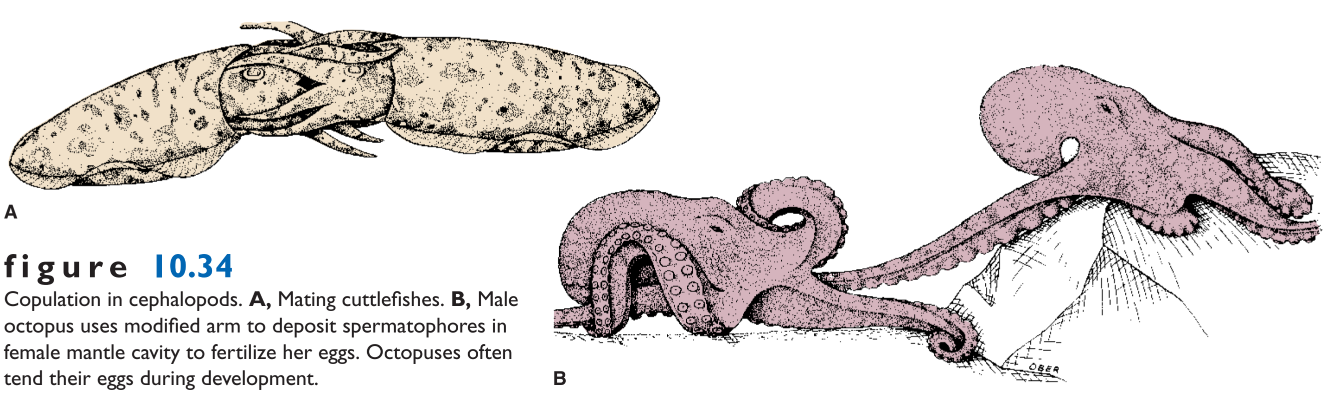


figure 10.34
Copulation in cephalopods. **A,** Mating cuttlefishes. **B,** Male octopus uses modified arm to deposit spermatophores in female mantle cavity to fertilize her eggs. Octopuses often tend their eggs during development.

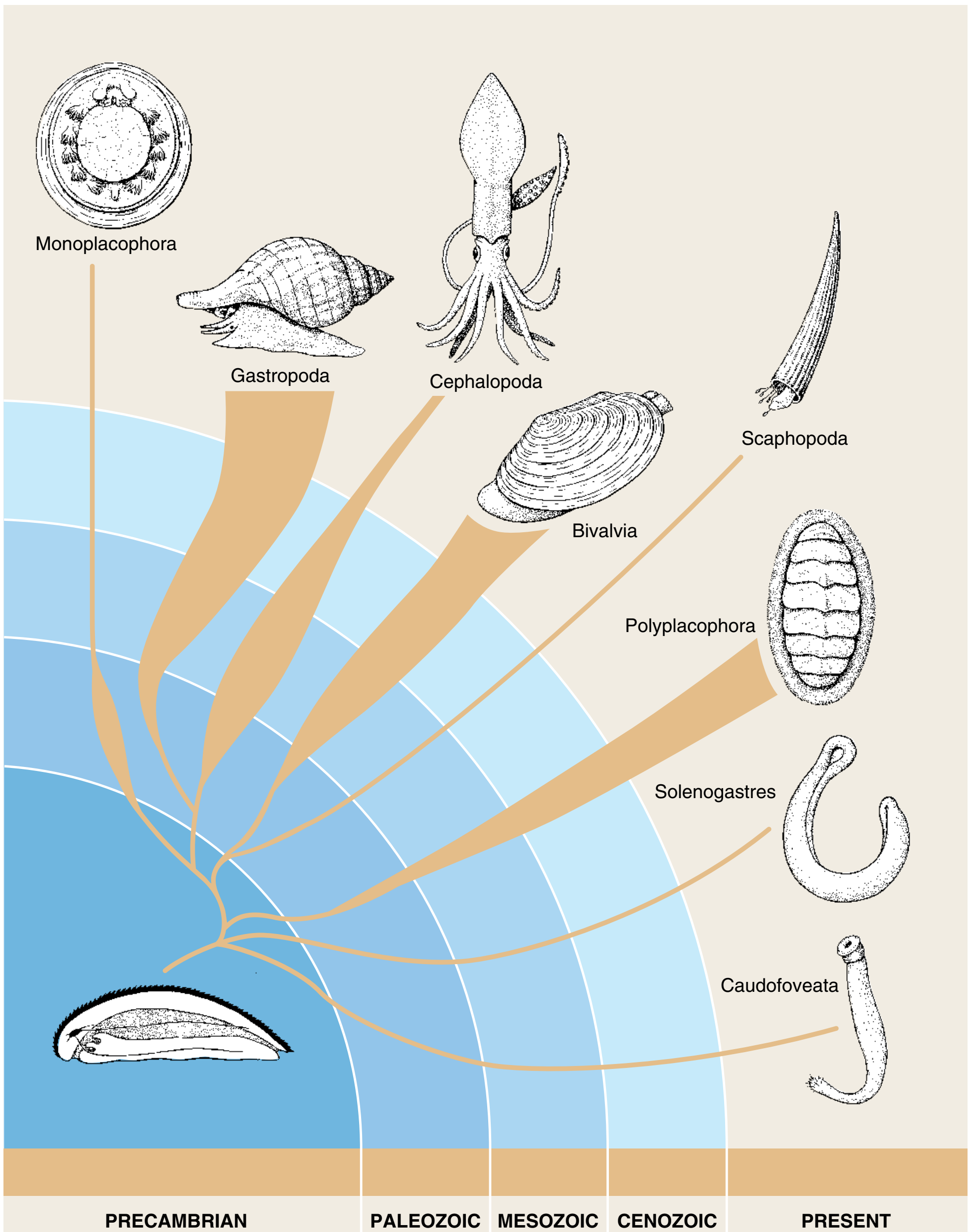


figure 10.35
Classes of Mollusca, showing their derivations and relative abundance.

foot is represented by the ventral groove. Both these classes probably branched from primitive ancestors before the development of a solid shell, a distinct head with sensory organs, and a ventral muscularized foot. Polyplacophorans probably also branched early from the main lines of molluscan evolution before the veliger was established as a larva. Some workers believe that shells of polyplacophorans are not homologous to shells of other molluscs because they differ structurally and developmentally. Polyplacophora and the remaining classes are sister groups (figure 10.36).

Cladistic analysis suggests that Gastropoda and Cephalopoda form the sister group to Monoplacophora (see figure 10.36). Both gastropods and cephalopods have a greatly expanded visceral mass. The mantle cavity was brought toward the head by torsion in gastropods, but in cephalopods the mantle cavity was extended ventrally. Evolution of a cham-

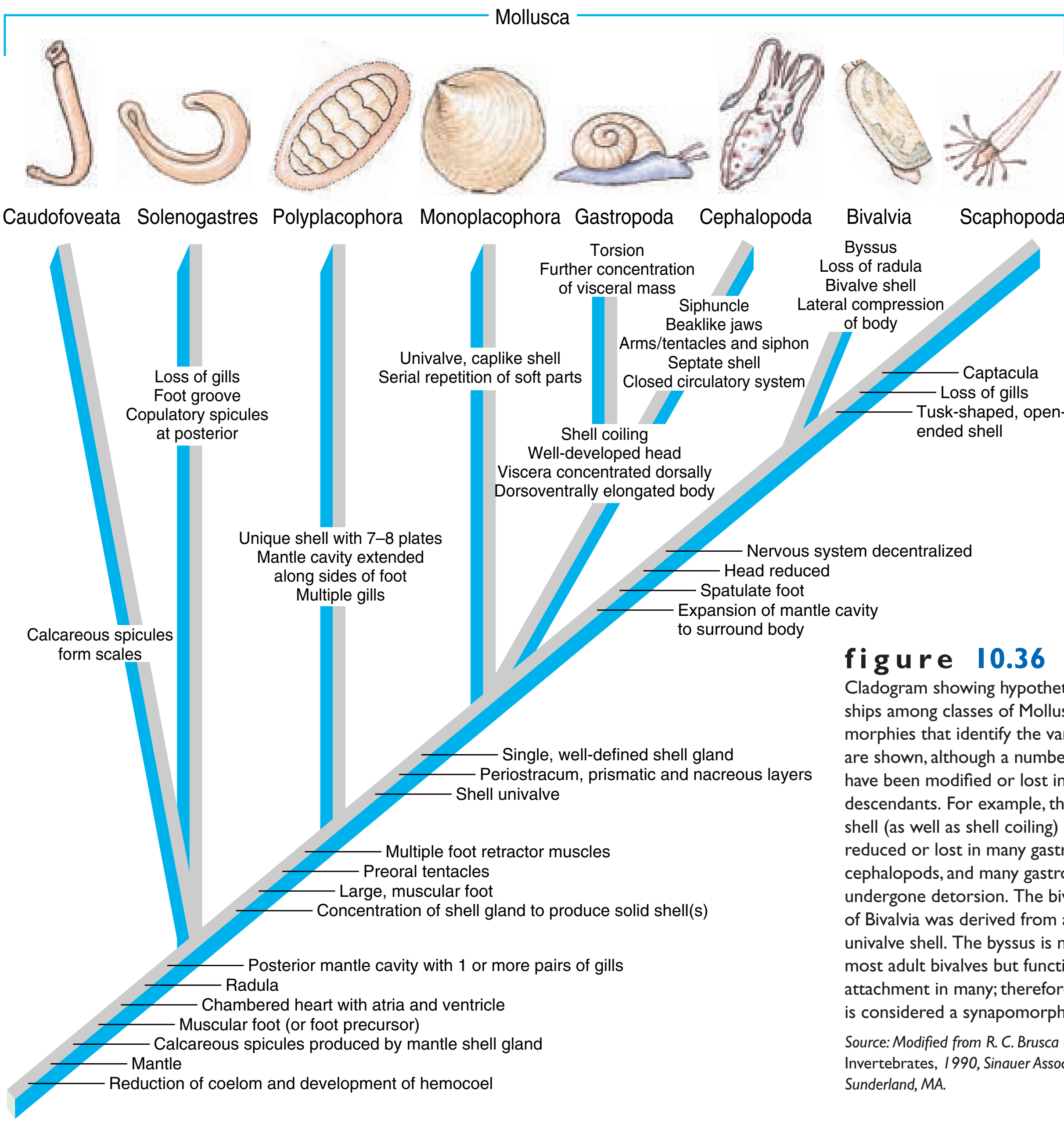


figure 10.36

Cladogram showing hypothetical relationships among classes of Mollusca. Synapomorphies that identify the various clades are shown, although a number of these have been modified or lost in some descendants. For example, the univalve shell (as well as shell coiling) has been reduced or lost in many gastropods and cephalopods, and many gastropods have undergone detorsion. The bivalve shell of Bivalvia was derived from an ancestral univalve shell. The byssus is not present in most adult bivalves but functions in larval attachment in many; therefore the byssus is considered a synapomorphy of Bivalvia.

Source: Modified from R. C. Brusca and G. J. Brusca, Invertebrates, *1990, Sinauer Associates, Inc., Sunderland, MA.*

bered shell in cephalopods was a very important contribution to their freedom from the substratum and their ability to swim. Elaboration of their respiratory, circulatory, and nervous systems is correlated with their predatory and swimming habits.

Scaphopods and bivalves have an expanded mantle cavity that essentially envelops the body. Adaptations for burrowing characterize this clade: spatulate foot and reduction of the head and sense organs.

Most diversity among molluscs is related to their adaptation to different habitats and modes of life and to a wide variety of feeding methods, ranging from sedentary filter feeding to active predation. There are many adaptations for food gathering within the phylum and an enormous variety in radular structure and function, particularly among gastropods.

The versatile glandular mantle has probably shown more plastic adaptive capacity than any other molluscan structure. Besides secreting the shell and forming the mantle cavity, it is variously modified into gills, lungs, siphons, and apertures, and it sometimes functions in locomotion, in feeding processes, or in a sensory capacity. The shell, too, has undergone a variety of evolutionary adaptations.

classification of phylum mollusca

Class Caudofoveata (kaw´do-fo-ve-at´a) (L. *cauda,* tail, + *fovea,* small pit): **caudofoveates.** Wormlike; shell, head, and excretory organs absent; radula usually present; mantle with chitinous cuticle and calcareous scales; oral pedal shield near anterior mouth; mantle cavity at posterior end with pair of gills; sexes separate; often united with solenogasters in class Aplacophora. Examples: *Chaetoderma, Limifossor.*

Class Solenogastres (so-len´o-gas´trez) (Gr. *solēn,* pipe, + *gastēr,* stomach): **solenogasters.** Wormlike; shell, head, and excretory organs absent; radula usually present; mantle usually covered with scales or spicules; mantle cavity posterior, without true gills, but sometimes with secondary respiratory structures; foot represented by long, narrow, ventral pedal groove; hermaphroditic. Example: *Neomenia.*

Class Monoplacophora (mon´o-pla-kof´o-ra) (Gr. *monos,* one, + *plax,* plate, + *phora,* bearing): **monoplacophorans.** Body bilaterally symmetrical with a broad flat foot; a single limpetlike shell; mantle cavity with five or six pairs of gills; large coelomic cavities; radula present; six pairs of nephridia, two of which are gonoducts; separate sexes. Example: *Neopilina* (see figure 10.7).

Class Polyplacophora (pol´y-pla-kof´o-ra) (Gr. *polys,* many, several, + *plax,* plate, + *phora,* bearing): **chitons.** Elongated, dorsoventrally flattened body with reduced head; bilaterally symmetrical; radula present; shell of eight dorsal plates; foot broad and flat; gills multiple, along sides of body between foot and mantle edge; sexes usually separate, with a trochophore but no veliger larva. Examples: *Mopalia* (see figure 10.8), *Chaetopleura.*

Class Scaphopoda (ska-fop´o-da) (Gr. *skaphē,* trough, boat, + *pous, podos,* foot): **tusk shells.** Body enclosed in a one-piece tubular shell open at both ends; conical foot; mouth with radula and tentacles; head absent; mantle for respiration; sexes separate; trochophore larva. Example: *Dentalium* (see figure 10.10).

Class Gastropoda (gas-trop´o-da) (Gr. *gastēr,* belly, + *pous, podos,* foot): **snails and relatives.** Body asymmetrical; usually in a coiled shell (shell uncoiled or absent in some); head well developed, with radula; foot large and flat; dioecious or monoecious, some with trochophore, typically with veliger, some without larva. Examples: *Busycon, Polinices* (see figure 10.14B), *Physa, Helix, Aplysia* (see figure 10.15).

Class Bivalvia (bi-val´ve-a) (L. *bi,* two, + *valva,* folding door, valve) **(Pelecypoda): bivalves.** Body enclosed in a two-lobed mantle; shell of two lateral valves of variable size and form, with dorsal hinge; head greatly reduced but mouth with labial palps; no radula; no cephalic eyes; gills platelike; foot usually wedge shaped; sexes usually separate, typically with trochophore and veliger larvae. Examples: *Mytilus* (see figure 10.27), *Venus, Bankia* (see figure 10.24).

Class Cephalopoda (sef´a-lop´o-da) (Gr. *kephalē,* head, + *pous, podos,* foot): **squids and octopuses.** Shell often reduced or absent; head well developed with eyes and a radula; head with arms or tentacles; foot modified into a funnel; nervous system of well-developed ganglia, centralized to form a brain; sexes separate, with direct development. Examples: *Loligo, Sepioteuthis* (see figure 10.30), *Octopus* (see figure 10.1E), *Sepia* (see figure 10.32), *Nautilus* (see figure 10.31).

summary

Mollusca is one of the largest and most diverse of all phyla, its members ranging in size from very small organisms to the largest of invertebrates. Their basic body divisions are the head-foot and the visceral mass, usually covered by a shell. The majority are marine, but some are freshwater, and a few are terrestrial. They occupy a variety of niches; a number are economically important, and a few are medically important as hosts of parasites.

Molluscs are coelomate (have a coelom), although their coelom is limited to the area around the heart. The evolutionary development of a coelom was important because it enabled better organization of visceral organs and, in many of the animals that have it, an efficient hydrostatic skeleton.

The mantle and mantle cavity are important characteristics of molluscs. The mantle secretes the shell and overlies a part of the visceral mass to form a cavity housing the gills. The mantle cavity has been modified into a lung in some molluscs. The foot is usually a ventral, solelike, locomotory organ, but it may be variously modified, as in the cephalopods, where it has become a funnel and arms. Most molluscs except bivalves and some solenogasters and gastropods have a radula, which is a protrusible, tonguelike organ with teeth used in feeding. Except in cephalopods, which have a closed circulatory system, the circulatory system of molluscs is open, with a heart and blood sinuses. Molluscs usually have a pair of nephridia connecting with the coelom and a complex nervous system with a variety of sense organs. The primitive larva of molluscs is the trochophore, and most marine molluscs have a more derived larva, the veliger.

Classes Caudofoveata and Solenogastres are small groups of wormlike molluscs with no shell. Scaphopoda is a slightly larger class with a tubular shell, open at both ends, and the mantle wrapped around the body.

Class Monoplacophora is a tiny, univalve marine group showing pseudometamerism or vestiges of true metamerism. Polyplacophora are more common and diverse marine organisms with shells in the form of a series of eight plates. They are rather sedentary animals with a row of gills along each side of their foot.

Gastropoda is the most successful and largest class of molluscs. Their interesting evolutionary history includes torsion, or the twisting of the posterior end to the anterior, so that the anus and head are at the same end, and coiling, an elongation and spiraling of the visceral mass. Torsion led to the survival problem of fouling, which is the release of excreta over the head and in front of the gills, and this problem was solved in various ways among different gastropods. Among the solutions to fouling were bringing water into one side of the mantle cavity and out the other (many gastropods), some degree of detorsion (opisthobranchs and pulmonates), and conversion of the mantle cavity into a lung (pulmonates).

Class Bivalvia is marine and freshwater, and their shell is divided into two valves joined by a dorsal ligament and held together by an adductor muscle. Most of them are suspension feeders, drawing water through their gills by ciliary action.

Members of class Cephalopoda are the most complex molluscs; they are all predators and many can swim rapidly. Their tentacles capture prey by adhesive secretions or by suckers. They swim by forcefully expelling water from their mantle cavity through a funnel, which was derived from the foot.

There is strong embryological and molecular evidence that molluscs share a common ancestor with annelids more recently than either of these phyla do with arthropods or deuterostome phyla, although molluscs are not metameric.

review questions

1. How does a coelom develop embryologically? Why was the evolutionary development of a coelom important?
2. Members of phylum Mollusca are extremely diverse, yet the phylum clearly constitutes a monophyletic group. What evidence can you cite in support of this statement?
3. How are molluscs important to humans?
4. Distinguish among the following classes of molluscs: Polyplacophora, Gastropoda, Bivalvia, Cephalopoda.
5. Define the following: radula, odontophore, periostracum, prismatic layer, nacreous layer, trochophore, veliger, glochidium, osphradium.
6. Briefly describe the habitat and habits of a typical chiton.
7. Define the following with respect to gastropods: operculum, torsion, fouling, bilateral asymmetry.
8. Torsion in gastropods created a selective disadvantage: fouling. Suggest one or more potential selective advantages that could have offset the disadvantage. How have gastropods evolved to avoid fouling?
9. Distinguish between opisthobranchs and pulmonates.
10. Briefly describe how a typical bivalve feeds and how it burrows.
11. What is the function of the siphuncle of cephalopods?
12. Describe how cephalopods swim and eat.
13. Cephalopods are actively swimming predators, but they evolved from a slow-moving, probably grazing ancestor. Describe evolutionary modifications of the ancestral plan that make the cephalopod life-style possible.
14. To what other major invertebrate groups are molluscs related, and what is the nature of the evidence for the relationship?
15. Briefly describe the characteristics of the hypothetical ancestral mollusc, and tell how each class of molluscs differs from the primitive condition with respect to each of the following: shell, radula, foot, mantle cavity and gills, circulatory system, head.

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