Position in Animal Kingdom

1. Phylum Echinodermata (e-ki no-der ma-ta) (Gr. *echinos,* sea urchin, hedgehog, *derma,* skin, *ata,* characterized by) belongs to the **Deuterostomia** branch of the animal kingdom, the members of which are enterocoelous coelomates. The other phyla traditionally assigned to this group are Chaetognatha, Hemichordata, and Chordata.
2. Primitively, deuterostomes have the following embryological features in common: anus developing from or near the blastopore, and mouth developing elsewhere; coelom budded off from the archenteron (enterocoel); radial and regulative (indeterminate) cleavage; and endomesoderm (mesoderm derived from or with the endoderm) from enterocoelic pouches.
3. Thus echinoderms, chordates, and hemichordates are presumably derived from a common ancestor. Nevertheless, their evolutionary history has taken the echinoderms to the point where they are very much unlike any other animal group.

Biological Contributions

1. There is one word that best describes echinoderms: strange. They have a unique constellation of characteristics found in no other phylum. Among the more striking features shown by echinoderms are as follows:
   a. A system of channels composing the **water-vascular system,** derived from a coelomic compartment.
   b. A **dermal endoskeleton** composed of calcareous ossicles.
   c. A **hemal system,** whose function remains mysterious, also enclosed in a coelomic compartment.
   d. Their **metamorphosis,** which changes a bilateral larva to a radial adult.

Echinoderms

Echinoderms are marine forms and include sea stars (also called starfishes), brittle stars, sea urchins, sea cucumbers, and sea lilies. They represent a bizarre group sharply distinguished from all other animals. Their name is derived from their external spines or protuberances. A calcareous endoskeleton is found in all members of the phylum, either in the form of plates or represented by scattered tiny ossicles.

The most noticeable characteristics of echinoderms are (1) spiny endoskeleton of plates, (2) water-vascular system, (3) pedicellariae, (4) dermal branchiae, and (5) radial or biradial symmetry. No other group with such complex organ systems has radial symmetry.

Echinoderms are an ancient group of animals extending back to the Cambrian period. Despite the excellent fossil record, the origin and early evolution of echinoderms are still obscure. It seems clear that they descend from bilateral ancestors because their larvae are bilateral but become radially symmetrical later in development. Many zoologists believe that early echinoderms were sessile and evolved radiality as an adaptation to sessile existence. Bilaterality is of adaptive value to animals that travel through their environment, while radiality is of value to animals whose environment meets them on all sides equally. Hence, the body plan of present-day echinoderms seems to have been derived from one that was attached to the bottom by a stalk, had radial symmetry and radiating grooves (ambulacra) for food gathering, and had an upward-facing oral side. Attached forms were once plentiful, but only about 80 species, all in class Crinoidea, still survive. Oddly, conditions have favored survival of their free-moving descendants, although they are still quite radial, and among them are some of the most abundant marine animals. Nevertheless, in the exception that proves the rule (that bilaterality is adaptive for free-moving animals), at least three groups of echinoderms (sea cucumbers and two groups of sea urchins) have evolved back toward bilaterality.

Echinoderms have no ability to osmoregulate and thus rarely venture into brackish waters. They occur in all oceans of the world and at all depths, from intertidal to abyssal regions. Often the most common animals in the deep ocean are echinoderms. The most abundant species found in the Philippine Trench (10,540 m) was a sea cucumber. Echinoderms are virtually all bottom dwellers, although there are a few pelagic species.

No parasitic echinoderms are known, but a few are commensals. On the other hand, a wide variety of other animals make their homes in or on echinoderms, including parasitic or commensal algae, protozoa, ctenophores, turbellarians, cirripedes, copepods, decapods, snails, clams, polychaetes, fish, and other echinoderms.

Asteroids, or sea stars (Figure 23-1), are commonly found on hard, rocky surfaces, but numerous species are at home on sandy or soft bottoms. Some species are particle feeders, but many are predators, feeding particularly on sedentary or sessile prey, since sea stars themselves are relatively slow moving.

Ophiuroids—brittle stars, or serpent stars (see Figure 23-11)—are by far the most active echinoderms, moving by their arms rather than by tube feet. A few species are reported to have swimming ability, and some burrow. They may be scavengers, browsers, or deposit or filter feeders. Some are commensal in large sponges, in whose water canals they may live in great numbers.
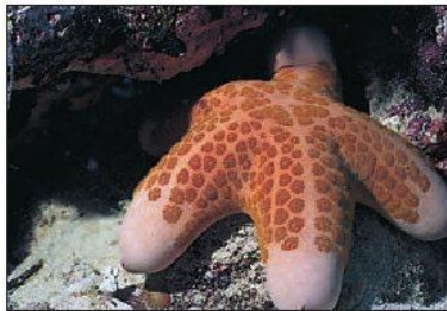
Holothurians, or sea cucumbers (see Figure 23-21), are widely prevalent in all seas. Many are found on sandy or mucky bottoms, where they lie concealed. Compared with other echinoderms, holothurians are greatly extended in the oral-aboral axis. They are oriented with that axis more or less

Characteristics of Phylum Echinodermata

1. Body unsegmented (nonmetameric) with **radial, pentamerous symmetry;** body rounded, cylindrical, or star shaped, with five or more radiating areas, or **ambulacra,** alternating with interambulacral areas
2. **No head or brain;** few specialized sensory organs; sensory system of tactile and chemoreceptors, podia, terminal tentacles, photoreceptors, and statocysts
3. Nervous system with circumoral ring and radial nerves; usually two or three systems of networks located at different levels in the body, varying in degree of development according to group
4. **Endoskeleton** of **dermal calcareous ossicles** with **spines** or of calcareous **spicules** in dermis; covered by an epidermis (ciliated in most); **pedicellariae** (in some)
5. A unique **water-vascular system** of coelomic origin that extends from the body surface as a series of tentacle-like projections **(podia,** or **tube feet)** that are protracted by increase of fluid pressure within them; an opening to the exterior **(madre-porite** or **hydropore)** usually present
6. Locomotion by tube feet, which project from the ambulacral areas, by movement of spines, or by movement of arms, which project from central disc of body
7. Digestive system usually complete; axial or coiled; anus absent in ophiuroids
8. Coelom extensive, forming the perivisceral cavity and the cavity of the water-vascular system; coelom of enterocoelous type; coelomic fluid with amebocytes
9. Blood-vascular system **(hemal system)** much reduced, playing little if any role in circulation, and surrounded by extensions of coelom **(perihemal sinuses);** main circulation of body fluids (coelomic fluids) by peritoneal cilia
10. Respiration by **dermal branchiae, tube feet, respiratory tree** (holothuroids), and **bursae** (ophiuroids)
11. **Excretory organs absent**
12. Sexes separate (except a few hermaphroditic) with large gonads, single in holothuroids but multiple in most; simple ducts, with no elaborate copulatory apparatus or secondary sexual structures; fertilization usually external; eggs brooded in some
13. Development through **free-swimming, bilateral, larval stages** (some with direct development); metamorphosis to radial adult or subadult form; radial cleavage and regulative development
14. Autotomy and regeneration of lost parts conspicuous

A

B

C

D

Figure 23-1

Some sea stars (class Asteroidea) from the Pacific. **A,** Cushion star *Pteraster tesselatus* can secrete incredible quantities of mucus as a defense. **B,** *Choriaster granulatus* scavenges dead animals on shallow Pacific reefs. **C,** *Tosia queenslandensis* from the Great Barrier Reef browses encrusting organisms. **D,** *Crossaster papposus,* rose star, feeds on other sea stars.

parallel to the substrate and lying on one side. Most are suspension or deposit feeders.

Echinoids, or sea urchins (see Figure 23-16), are adapted for living on the ocean bottom and always keep their oral surface in contact with the substratum. "Regular" sea urchins prefer hard bottoms, but sand dollars and heart urchins ("irregular" urchins) are usually found on sand. Regular urchins, which are radially symmetrical, feed chiefly on algae or detritus, while irregulars, which are secondarily bilateral, feed on small particles.

Crinoids (see Figure 23-26) stretch their arms out and up like a flower's petals and feed on plankton and suspended particles. Most living species become detached from their stems as adults, but they nevertheless spend most of their time on the substrate, holding on by means of aboral appendages called cirri.

The zoologist who admires the fascinating structure and function of echinoderms can share with the

layperson an admiration of the beauty of their symmetry, often enhanced by bright colors. Many species are rather drab, but others may be orange, red, purple, blue, and often multicolored.

Because of the spiny nature of their structure, echinoderms are not often prey of other animals—except other echinoderms (sea stars). Some fishes have strong teeth and other adaptations that enable them to feed on echinoderms. A few mammals, such as sea otters, feed on sea urchins. In scattered parts of the world, humans relish sea urchin gonads, either raw or roasted on the half shell. Trepang, the cooked, protein-rich body wall of certain large sea cucumbers, is a delicacy in many east Asian countries. Unfortunately, the intense, often illegal, fishery for sea cucumbers has severely depleted their populations in many areas of the tropical world.

Sea stars feed on a variety of molluscs, crustaceans, and other invertebrates. In some areas they may perform an important ecological role as a top carnivore in the habitat. Their chief economic impact is on clams and oysters. A single starfish may eat as many as a dozen oysters or clams in a day. To rid shellfish beds of these pests, quicklime is sometimes spread over areas where they abound. Quicklime

damages the delicate epidermal membrane, destroying the dermal branchiae and ultimately the animal itself. Unfortunately, other soft-bodied invertebrates are also damaged. However, the oysters remain with their shells tightly closed until the quicklime is degraded.

Echinoderms have been widely used in developmental studies, for their gametes are usually abundant and easy to collect and handle in the laboratory. Investigators can follow embryonic developmental stages with great accuracy. We know more about the molecular biology of sea urchin development than that of almost any other embryonic system. Artificial parthenogenesis was first discovered in sea urchin eggs, when it was found that, by treating eggs with hypertonic seawater or subjecting them to a variety of other stimuli, development would proceed without sperm.

Class Asteroidea

Sea stars, often called starfishes, demonstrate the basic features of echinoderm structure and function very well, and they are easily obtainable. Thus we will consider them first, then comment on major differences shown by other groups.
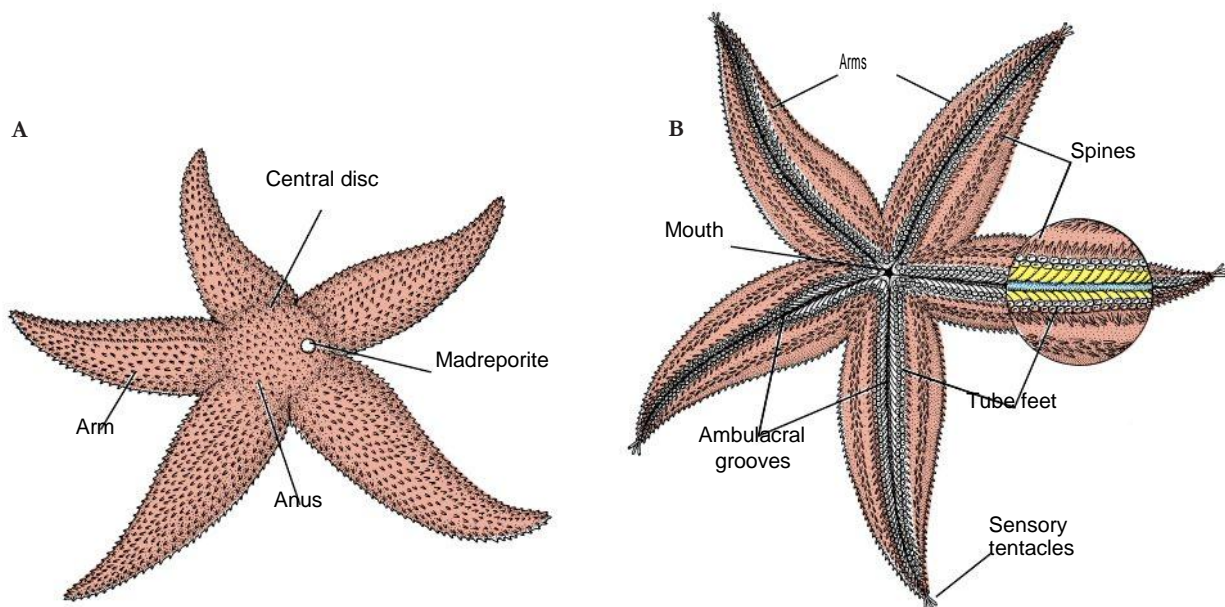
Sea stars are familiar along the

shoreline where large numbers may aggregate on rocks. Sometimes they cling so tenaciously that they are difficult to dislodge without tearing off some tube feet. They also live on muddy or sandy bottoms and among coral reefs. They are often brightly colored and range in size from a centimeter in greatest diameter to about a meter across. *Asterias* (Gr. *asteros,* a star) is one of the common genera of the east coast of the United States and is commonly studied in zoology laboratories. *Pisaster* (Gr. *pisos,* a pea, *asteros,* a star) is common on the west coast of the United States, as is *Dermasterias* (Gr. *dermatos,* skin, leather, *asteros,* a star), the leather star.
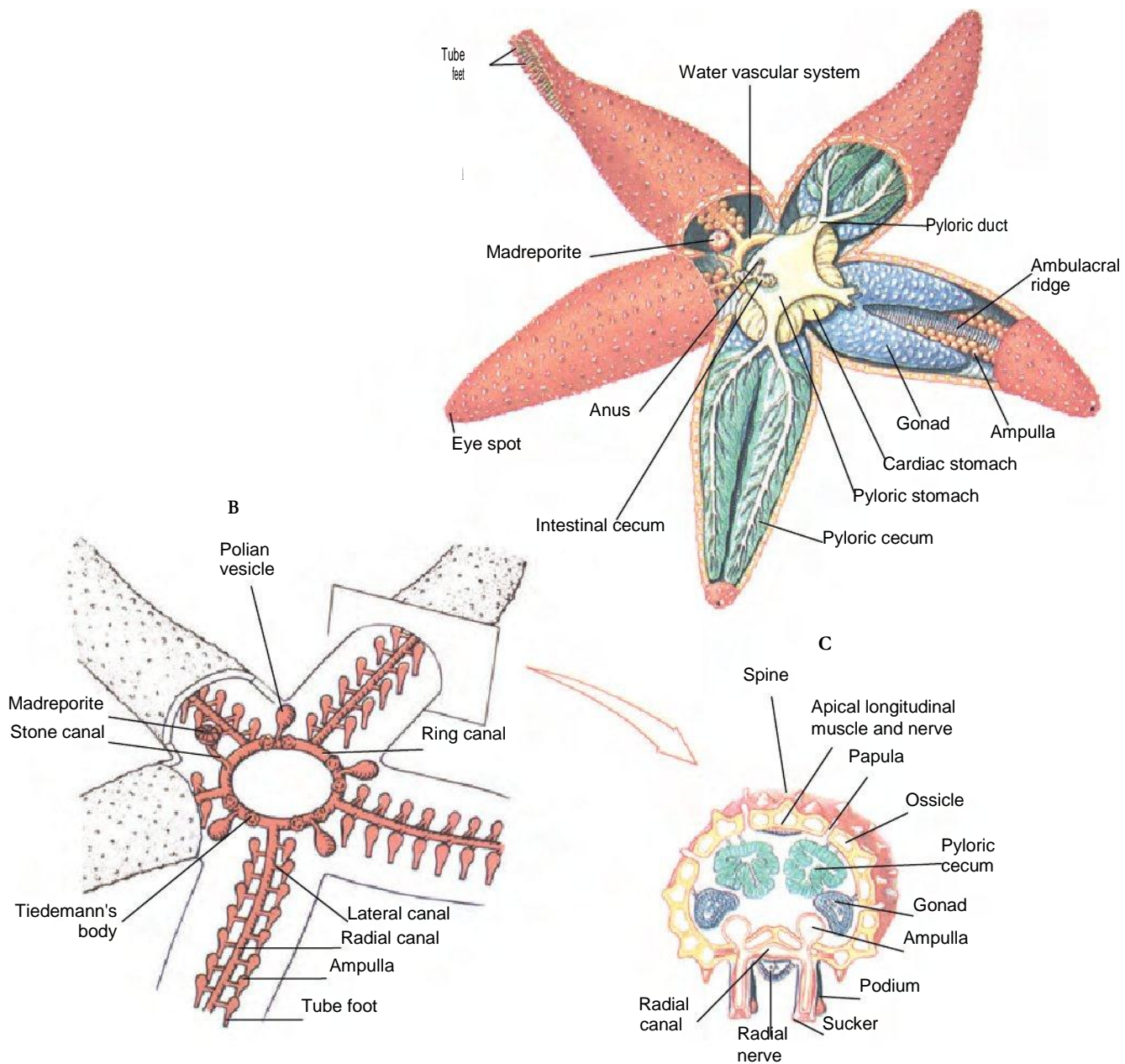
Form and Function
External Features

Sea stars are composed of a central disc that merges gradually with the tapering arms (rays). The body is somewhat flattened, flexible, and covered with a ciliated, pigmented epidermis. The mouth is centered on the under, or oral, side, surrounded by a soft peristomial membrane. An **ambulacrum** (pl., **ambulacra,** *L. ambulacrum,* a covered way, an alley, a walk planted with trees) or **ambulacral area,** runs from the mouth on

Figure 23-2
External anatomy of asteroid. **A,** Aboral view. **B,** Oral view.

Figure 23-3

A, Internal anatomy of a sea star. **B,** Water-vascular system. Podia penetrate between ossicles. (Polian vesicles are not present in *Asterias.*) **C,** Cross section of arm at level of gonads, illustrating open ambulacral grooves.
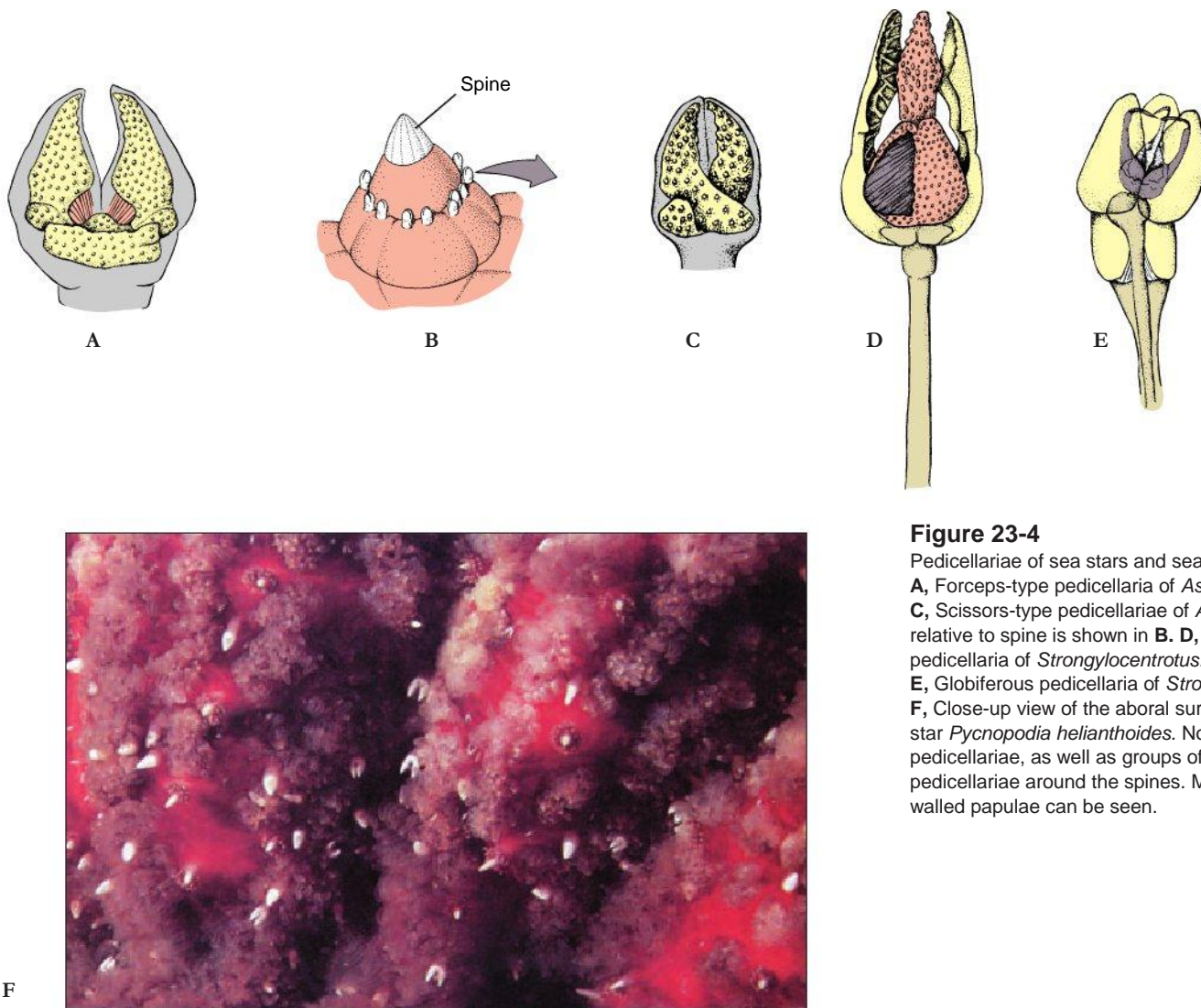
the oral side of each arm to the tip of the arm. Sea stars typically have five arms, but they may have more (Figure 23-1D), and there are as many ambulacral areas as there are arms. An **ambulacral groove** is found along the middle of each ambulacral area, and the groove is bordered by rows of **tube feet (podia)** (Figure 23-2). These in turn are usually protected by movable **spines.** A large **radial nerve** can be seen in the center of each ambu-

lacral groove (Figure 23-3C), between the rows of tube feet. The nerve is very superficially located, covered only by thin epidermis. Under the nerve is an extension of the coelom and the radial canal of the water-vascular system, all of which are external to the underlying ossicles (Figure 23-3C). In all other classes of living echinoderms except crinoids, these structures are covered by ossicles or other dermal tissue; thus ambulacral grooves in asteroids and

crinoids are said to be *open,* and those of the other groups are *closed.*

The aboral surface is usually rough and spiny, although spines of many species are flattened, so that the surface appears smooth (Figure 23-1C). Around the bases of spines are groups of minute, pincerlike **pedicellariae,** bearing tiny jaws manipulated by muscles (Figure 23-4). These jaws help keep the body surface free of debris, protect the papulae, and sometimes

Spine

A   B   C   D   E

Figure 23-4
Pedicellariae of sea stars and sea urchins.
A, Forceps-type pedicellaria of *Asterias*. **B,** and
C, Scissors-type pedicellariae of *Asterias;* size
relative to spine is shown in **B. D,** Tridactyl
pedicellaria of *Strongylocentrotus.*
E, Globiferous pedicellaria of *Strongylocentrotus.*
F, Close-up view of the aboral surface of the sea
star *Pycnopodia helianthoides.* Note the large
pedicellariae, as well as groups of small
pedicellariae around the spines. Many thin-
walled papulae can be seen.

F

aid in food capture. **Papulae (dermal branchiae** or **skin gills)** are soft delicate projections of the coelomic cavity, covered only with epidermis and lined internally with peritoneum; they extend out through spaces between ossicles and are concerned with respiration (Figures 23-3C, and 23-4F). Also on the aboral side are the inconspicuous anus and the circular **madreporite** (Figure 23-2A), a calcareous sieve leading to the water-vascular system.

Endoskeleton

Beneath the epidermis of sea stars is a mesodermal endoskeleton of small calcareous plates, or **ossicles,** bound together with connective tissue. From these ossicles project the spines and

tubercles that make up the spiny surface. Ossicles are penetrated by a meshwork of spaces, usually filled with fibers and dermal cells. This internal meshwork structure is described as **stereom** and is unique to echinoderms.

Muscles in the body wall move the rays and can partially close the ambulacral grooves by drawing their margins together.

Coelom, Excretion, and Respiration

The coelomic compartments of larval echinoderms give rise to several structures in adults, one of which is a spacious body coelom filled with fluid. The fluid contains amebocytes (coelomocytes), bathes the internal organs,

and projects into the papulae. The ciliated peritoneal lining of the coelom circulates the fluid around the body cavity and into the papulae. Exchange of respiratory gases and excretion of nitrogenous waste, principally ammonia, take place by diffusion through the thin walls of papulae and tube feet. Some wastes may be picked up by coelomocytes, which migrate through the epithelium of the papulae or tube feet to the exterior, or the tips of papulae containing waste-laden coelomocytes may pinch off.

Water-Vascular System

The water-vascular system is another coelomic compartment and is unique to echinoderms. Showing exploitation of hydraulic mechanisms to a greater

degree than in any other animal group, it is a system of canals and specialized tube feet that, together with the dermal ossicles, has determined the evolutionary potential and limitations of this phylum. In sea stars the primary functions of the water-vascular system are locomotion and food gathering, in addition to respiration and excretion.

Structurally, the water-vascular system opens to the outside through small pores in the madreporite. The madreporite of asteroids is on the aboral surface (Figure 23-2A) and leads into the **stone canal,** which descends toward the **ring canal** around the mouth (Figure 23-3B). **Radial canals** diverge from the ring canal, one into the ambulacral groove of each ray. Also attached to the ring canal are four or five pairs of folded, pouchlike **Tiedemann's bodies** and from one to five **polian vesicles** (polian vesicles are absent in some sea stars, such as *Asterias).* Tiedemann's bodies may produce coelomocytes, and polian vesicles are apparently for fluid storage.

A series of small **lateral canals,** each with a one-way valve, connects the radial canal to the cylindrical podia, or tube feet, along the sides of the ambulacral groove in each ray. Each podium is a hollow, muscular tube, the inner end of which is a muscular sac, or **ampulla,** that lies within the body coelom (Figure 23-3A and C), and the outer end of which usually bears a **sucker.** Some species lack suckers. Podia pass to the outside between ossicles in the ambulacral groove.

The water-vascular system operates hydraulically and is an effective locomotor mechanism. The valves in the lateral canals prevent backflow of fluid into the radial canals. Each tube foot has in its walls connective tissue that maintains the cylinder at a relatively constant diameter. Contraction of muscles in the ampulla forces fluid into the podium, extending it. Conversely, contraction of the longitudinal muscles in the tube foot retracts the podium, forcing fluid back into the ampulla. Contraction of muscles in one side of the podium bends the organ toward that side. Small muscles at the end of the

A   B

Figure 23-5
A, *Orthasterias koehleri* eating a clam. **B,** This *Pycnopodia helianthoides* has been overturned while eating a large sea urchin *Strongylocentrotus franciscanus.* This sea star has 20 to 24 arms and can range up to 1 m in diameter (arm tip to arm tip).

tube foot can raise the middle of the disclike end, creating suction when the end is applied to a firm substrate. It has been estimated that by combining mucous adhesion with suction, a single podium can exert a pull equal to 25 to 30 g. Coordinated action of all or many of the tube feet is sufficient to draw the animal up a vertical surface or over rocks. The ability to move while firmly adhering to the substrate is a clear advantage to an animal living in a sometimes wave-churned environment.

On a soft surface, such as muck or sand, suckers are ineffective (numerous sand-dwelling species have no suckers), so the tube feet are employed as legs. Locomotion becomes mainly a stepping process. Most sea stars can move only a few centimeters per minute, but some very active ones can move 75 to 100 cm per minute; for example, *Pycnopodia* (Gr. *pyknos,* compact, dense,   *pous, podos,* foot) (Figure 23-5B). When inverted, a sea star bends its rays until some of the tubes reach the substratum and attach as an anchor; then it slowly rolls over.

Tube feet are innervated by the central nervous system (ectoneural and hyponeural systems, see following text). Nervous coordination enables tube feet to move in a single direction, although not in unison, so that the sea

star may progress. If the radial nerve in an arm is cut, podia in that arm lose coordination, although they can still function. If the circumoral nerve ring is cut, podia in all arms become uncoordinated, and movement ceases.

Feeding and Digestive System

The mouth on the oral side leads through a short esophagus to a large stomach in the central disc. The lower (cardiac) part of the stomach can be everted through the mouth during feeding (Figure 23-2B), and excessive eversion is prevented by gastric ligaments. The upper (pyloric) part is smaller and connects by ducts to a pair of large **pyloric ceca (digestive glands)** in each arm (Figure 23-3A). Digestion is mostly extracellular, although some intracellular digestion may occur in the ceca. A short intestine leads aborally from the pyloric stomach, and there are usually a few small, saclike **intestinal ceca** (Figure 23-3A). The anus is inconspicuous, and some sea stars lack an intestine and anus.

Many sea stars are carnivorous and feed on molluscs, crustaceans, polychaetes, echinoderms, other invertebrates, and sometimes small fish. Sea stars consume a wide range of food items, but many show particular
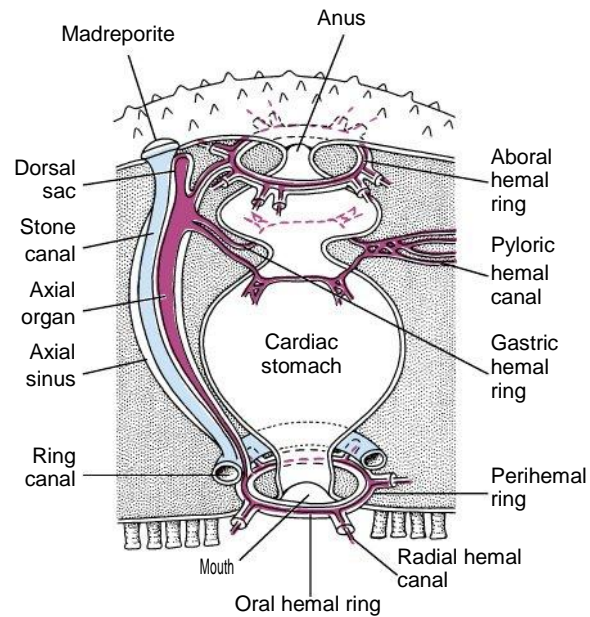
Figure 23-6
Crown-of-thorns star *Acanthaster planci* feeding on coral. Puncture wounds from its spines are painful; the spines are equipped with poison glands.

Figure 23-7
Hemal system of asteroids. The main perihemal channel is the thin-walled axial sinus, which encloses both the axial organ and the stone canal. Other features of the hemal system are shown.

preferences (Figures 23-5 and 23-6). Some select brittle stars, sea urchins, or sand dollars, swallowing them whole and later regurgitating undigestible ossicles and spines (Figure 23-5B). Some attack other sea stars, and if they are small compared with their prey, they may attack and begin eating at the end of one arm.

Since 1963 there have been numerous reports of increasing numbers of the crown-of-thorns starfish (Acanthaster *planci* [Gr. *akantha,* thorn,   *asteros,* star]) (Figure 23-6) that were damaging large areas of coral reef in the Pacific Ocean. Crown-of-thorns stars feed on coral polyps, and they sometimes occur in large aggregations, or "herds." There is some evidence that outbreaks have occurred in the past, but an increase in frequency during the past 30 years suggests that some human activity may be affecting the starfish. Efforts to control the organism are very expensive and of questionable effectiveness.The controversy continues, especially in Australia, where it is exacerbated by extensive media coverage.

Some asteroids feed heavily on molluscs (Figure 23-5A), and *Asterias* is a significant predator on commercially important clams and oysters. When feeding on a bivalve, a sea star will hump over its prey, attaching its podia to the valves, and then exert a steady pull, using its feet in relays. A force of some 1300 g can thus be exerted. In half an hour or so the adductor muscles of the bivalve fatigue and relax. With a very small gap available, the star inserts its soft everted stomach into the space between the valves and wraps it around the soft parts of the shellfish. After feeding, the sea star draws its stomach inward by contraction of the stomach muscles and relaxation of body-wall muscles.

Some sea stars feed on small particles, either entirely or in addition to carnivorous feeding. Plankton and other organic particles coming in contact with the animal's surface are carried by the epidermal cilia to the ambulacral grooves and then to the mouth.

Hemal System

The so-called hemal system is not very well developed in asteroids, and its function in all echinoderms is unclear. The hemal system has little or nothing to do with circulation of body fluids. It is a system of tissue strands enclosing unlined sinuses and is itself enclosed in another coelomic compartment, the **perihemal channels** (Figure 23-7). The hemal system may be useful in distributing digested products, but its specific functions are not really known.

Nervous System

The nervous system consists of three units at different levels in the disc and arms. Chief of these systems is the **oral (ectoneural)** system composed of a **nerve ring** around the mouth and a main **radial nerve** into each arm. It appears to coordinate the tube feet. A **deep (hyponeural)** system lies aboral to the oral system, and an **aboral** system consists of a ring around the anus and radial nerves along the roof of each ray. An **epidermal nerve plexus** or nerve net freely connects these systems with the body wall and related structures. The epidermal plexus coordinates responses of the dermal branchiae to tactile stimulation—the

only instance known in echinoderms in which coordination occurs through a nerve net.

Sense organs are not well developed. Tactile organs and other sensory cells are scattered over the surface, and an ocellus is at the tip of each arm. Their reactions are mainly to touch, temperature, chemicals, and differences in light intensity. Sea stars are usually more active at night.

Reproductive System, Regeneration, and Autotomy

Most sea stars have separate sexes. A pair of gonads lies in each interradial space (Figure 23-3A). Fertilization is external and occurs in early summer when eggs and sperm are shed into the water. A secretion from neurosecretory cells located on the radial nerves stimulates maturation and shedding of asteroid eggs.
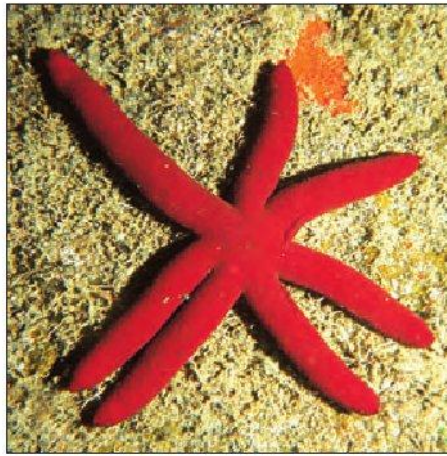
Echinoderms can regenerate lost parts. Sea star arms can regenerate readily, even if all are lost. Sea stars also have the power of autotomy and can cast off an injured arm near the base. Regeneration of a new arm may take several months.

Some species can regenerate a complete new sea star (Figure 23-8) from a detached arm that contains a part (about one-fifth) of the central disc. In former times fishermen used to dispatch sea stars they collected from their oyster beds by chopping them in half with a hatchet—a worse than futile activity. Some sea stars reproduce asexually under normal conditions by cleaving the central disc, each part regenerating the rest of the disc and missing arms.

Development

In some species the liberated eggs are brooded, either under the oral side of the animal or in specialized aboral structures, and development is direct, but in most species embryonating eggs are free in the water and hatch to free-swimming larvae.

Early embryogenesis shows a typical primitive deuterostome pattern (see

Figure 23-8
Pacific sea star *Echinaster luzonicus* can reproduce itself by splitting across the disc, then regenerating missing arms. The one shown here has evidently regenerated six arms from the longer one at top left.

Figures 8-7A and 8-11A). Gastrulation is by invagination, and the anterior end of the archenteron pinches off to become the coelomic cavity, which expands in a U shape to fill the blastocoel. Each of the legs of the U, at the posterior, constricts to become a separate vesicle, and these eventually give rise to the main coelomic compartments of the body (metacoels, called **somatocoels** in echinoderms). The anterior portion of the U undergoes subdivision to form the protocoels and mesocoels (called **axocoels** and **hydrocoels** in echinoderms) (Figure 23-9). The left hydrocoel will become the water-vascular system, and the left axocoel will give rise to the stone canal and perihemal channels. The right axocoel and hydrocoel will disappear. The free-swimming larva has cilia arranged in bands and is called a **bipinnaria** (Figure 23-10A). These ciliated tracts become extended into larval arms. Soon the larva grows three adhesive arms and a sucker at its anterior end and is then called a **brachiolaria.** At that time it attaches to the substratum, forms a temporary attachment stalk, and undergoes metamorphosis.

Metamorphosis involves a dramatic reorganization of a bilateral larva into a radial juvenile. The anteroposterior axis of the larva is lost, and *what was the left side becomes the oral sur-*

face, and the larval right side becomes the aboral surface (Figure 23-9). Correspondingly, the larval mouth and anus disappear, and a new mouth and anus form on what were originally the left and right sides, respectively. The portion of the anterior coelomic compartment from the left side expands to form the ring canal of the water-vascular system around the mouth, and then it grows branches to form the radial canals. As the short, stubby arms and the first podia appear, the animal detaches from its stalk and begins life as a young sea star.
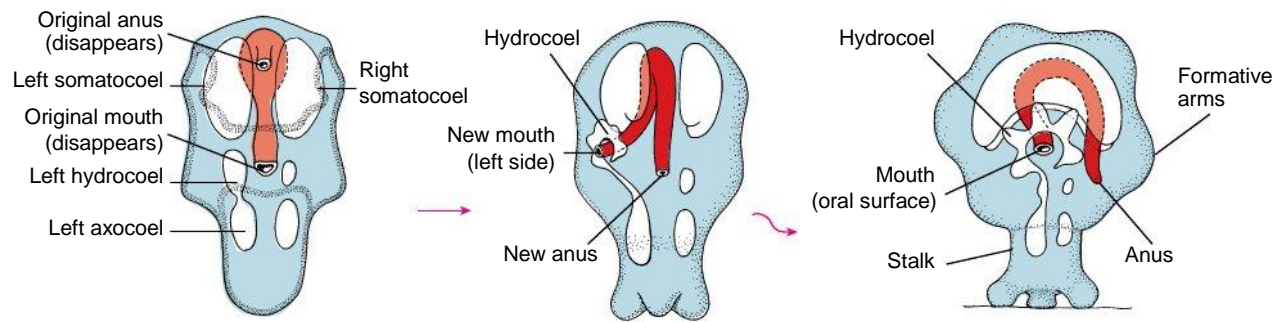
Class Ophiuroidea

Brittle stars are largest of the major groups of echinoderms in numbers of species, and they are probably the most abundant also. They abound in all types of benthic marine habitats, even carpeting the abyssal sea bottom in many areas.
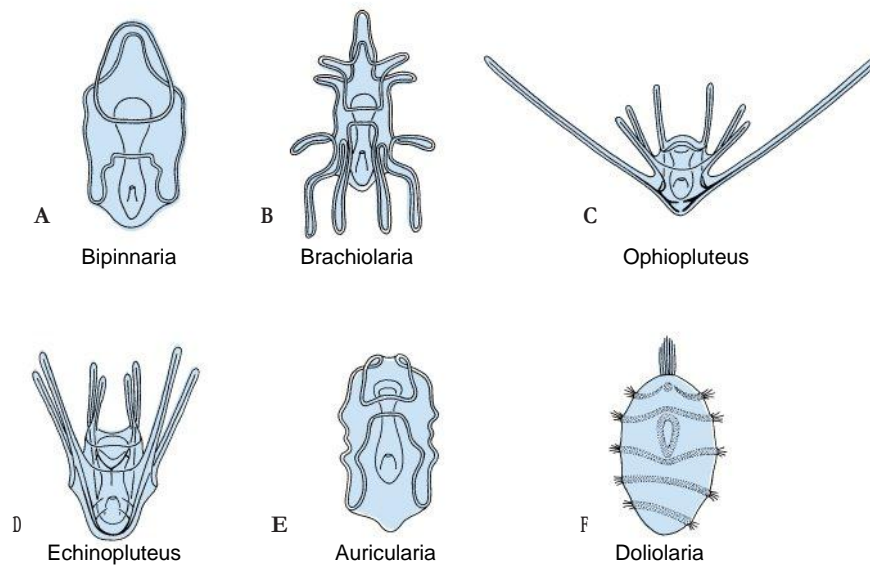
Form and Function

Apart from the typical possession of five arms, brittle stars are surprisingly different from asteroids. The arms of brittle stars are slender and sharply set off from the central disc (Figure 23-11). They have no pedicellariae or papulae, and their ambulacral grooves are closed and covered with arm ossicles. Their tube feet are without suckers; they aid in feeding but are of limited use in locomotion. In contrast to asteroids, the madreporite of ophiuroids is located on the oral surface, on one of the oral shield ossicles (Figure 23-12). Ampullae on the podia are absent, and force for protrusion of the podium is generated by a proximal muscular portion of the podium.

Each jointed arm consists of a column of articulated ossicles (the so-called **vertebrae),** connected by muscles and covered by plates. Locomotion is by arm movement. Arms are moved forward in pairs and are placed against the substratum, while one (any one) is extended forward or trailed behind, and the animal is pulled or pushed along in a jerky fashion.

Figure 23-9
Asteroid metamorphosis. The left somatocoel becomes the oral coelom, and the right somatocoel becomes the aboral coelom. The left hydrocoel becomes the water-vascular system and the left axocoel the stone canal and perihemal channels. The right axocoel and hydrocoel are lost.

Figure 23-10
Larvae of echinoderms. **A,** Bipinnaria of asteroids. **B,** Brachiolaria of asteroids. **C,** Ophiopluteus of ophiuroids. **D,** Echinopluteus of echinoids. **E,** Auricularia of holothuroids. **F,** Doliolaria of crinoids.

Figure 23-11
A, Brittle star *Ophiura lutkeni* (class Ophiuroidea). Brittle stars do not use their tube feet for locomotion but can move rapidly (for an echinoderm) by means of their arms. **B,** Basket star *Astrophyton muricatum* (class Ophiuroidea). Basket stars extend their many-branched arms to filter feed, usually at night.

Five movable plates that serve as jaws surround the mouth (Figure 23-12). There is no anus. The skin is leathery, with dermal plates and spines arranged in characteristic patterns. Surface cilia are mostly lacking.

The visceral organs are confined to the central disc, since the rays are too slender to contain them (Figure 23-13). The stomach is saclike, and there is no intestine. Indigestible material is cast out of the mouth.
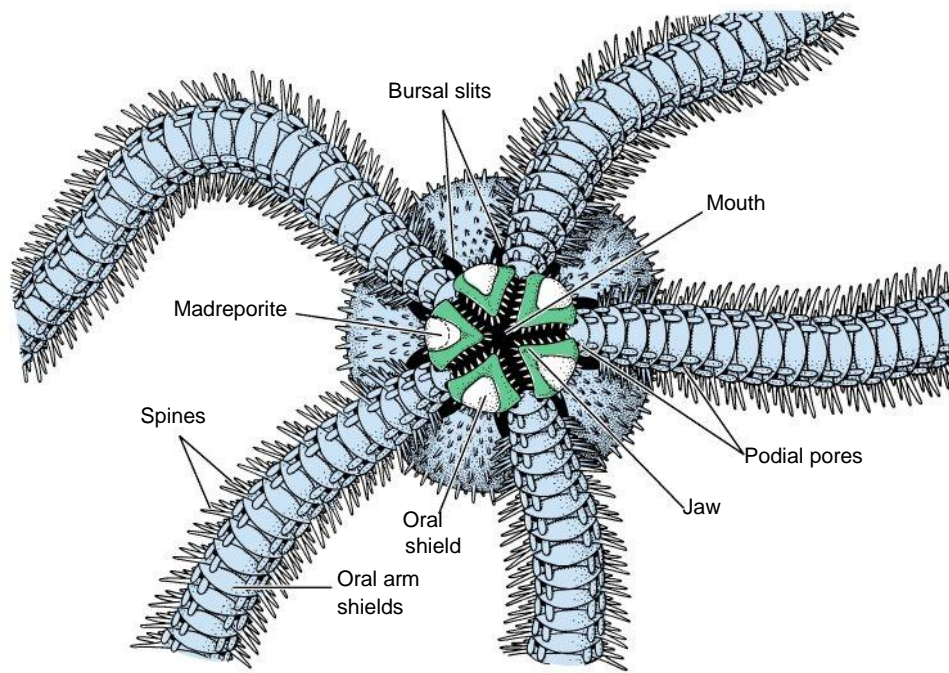
Five pairs of invaginations called **bursae** open toward the oral surface by genital slits at the bases of the arms. Water circulates in and out of these sacs for exchange of gases. On the coelomic wall of each bursa are small gonads that discharge into the bursa their ripe sex cells, which pass through the genital slits into the water for fertilization (Figure 23-14A). Sexes are usually separate; a few ophiuroids are hermaphroditic. Some brood their young in the bursae; the young escape through the genital slits or by rupturing the aboral disc. The larva is called an ophiopluteus, and its ciliated bands extend onto delicate, beautiful larval arms (Figure 23-10C). During metamorphosis to a juvenile, there is no temporarily attached phase, as there is in asteroids.

Water-vascular, nervous, and hemal systems are similar to those of sea stars. Each arm contains a small coelom, a radial nerve, and a radial canal of the water-vascular system.
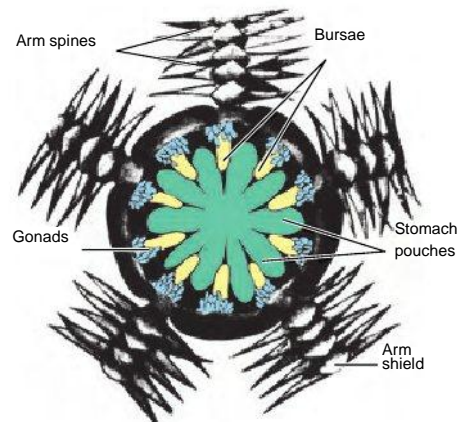
Biology

Brittle stars tend to be secretive, living on hard bottoms where little or no light penetrates. They are generally

Figure 23-12
Oral view of spiny brittle star *Ophiothrix.*

Figure 23-13
Ophiuroid with aboral disc wall cut away to show principal internal structures. The bursae are fluid-filled sacs in which water constantly circulates for respiration. They also serve as brood chambers. Only bases of arms are shown.

Figure 23-14
A, This brittle star *Ophiopholis aculeata* has its bursae swollen with eggs, which it is ready to expel. The arms have been broken and are regenerating. **B,** Oral view of a basket star *Gorgonocephalus eucnemis,* showing pentaradial symmetry.

Figure 23-15
Purple sea urchin *Strongylocentrotus purpuratus* is common along the Pacific coast of North America where there is heavy wave action.
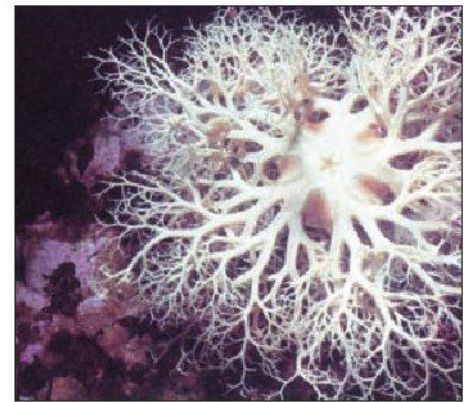
sion feeding. Podia are important in transferring food to the mouth. Some brittle stars extend arms into the water and catch suspended particles in mucous strands between arm spines.

Regeneration and autotomy are even more pronounced in brittle stars than in sea stars. Many seem very fragile, releasing an arm or even part of the disc at the slightest provocation. Some can reproduce asexually by cleaving the disc; each progeny then regenerates the missing parts.

Some common ophiuroids along the coast of the United States are *Amphipholis* (Gr. *amphi,* both sides of, *pholis,* horny scale) (viviparous and hermaphroditic), *Ophioderma* (Gr. *ophis,* snake, *dermatos,* skin), *Ophiothrix* (Gr. *ophis,* snake, *thrix,* hair), and *Ophiura* (Gr. *ophis,* snake, *oura,* tail) (Figure 23-11). The basket stars *Gorgonocephalus* (Gr. *Gorgo,* name of a female monster of terrible aspect, *kephalē,* a head) (Figure 23-14B) and *Astrophyton* (Gr. *asteros,* star, *phyton,* creature, animal) (Figure 23-11B) have arms that branch repeatedly. Most ophiuroids are drab, but some are attractive, with bright color patterns (Figure 23-14A).
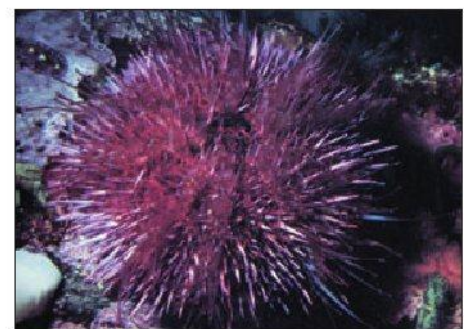
negatively phototropic and insinuate themselves into small crevices between rocks, becoming more active at night. They are commonly fully exposed on the bottom in the permanent darkness of the deep sea. Ophiuroids feed on a variety of small particles, either browsing food from the bottom or suspen-

Class Echinoidea

Echinoids have a compact body enclosed in an endoskeletal test, or shell. Dermal ossicles, which have become
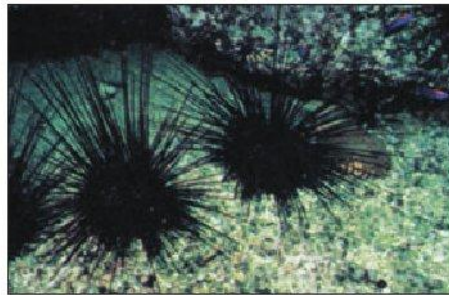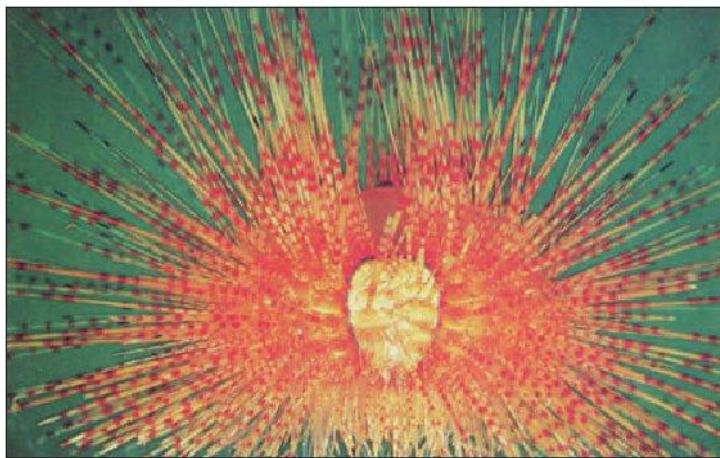
A

B

C

D

E

Figure 23-16

Diversity among regular sea urchins (class Echinoidea). **A,** Pencil urchin *Eucidaris tribuloides.* Members of this order have many primitive characters and have survived since the Paleozoic era. They may be closest in resemblance to the common ancestor of all other extant echinoids. **B,** Slate-pencil urchin *Heterocentrotus mammilatus.* The large, triangular spines of this urchin were formerly used for writing on slates. **C,** Aboral spines of the intertidal urchin *Colobocentrotus atratus* are flattened and mushroom shaped, while the marginal spines are wedge shaped, giving the animal a streamlined form to withstand pounding surf. **D,** *Diadema antillarum* is a common species in the West Indies and Florida. **E,** *Astropyga magnifica* is one of the most spectacularly colored sea urchins, with bright-blue spots along its interambulacral areas.

closely fitting plates, make up the test. Echinoids lack arms, but their tests reflect the typical pentamerous plan of echinoderms in their five ambulacral areas. The most notable modification of the ancestral body plan is that the oral surface has expanded around to the aboral side, so that the ambulacral

areas extend up to the area around the anus **(periproct).** The majority of living species of sea urchins are "regular"; they have a hemispherical shape, radial symmetry, and medium to long spines (Figures 23-15 and 23-16). Sand dollars (Figure 23-17) and heart urchins (Figure 23-18) are "irregular" because the

orders to which they belong have become secondarily bilateral; their spines are usually very short. Regular urchins move by means of their tube feet, with some assistance from their spines, and irregular urchins move chiefly by their spines (Figure 23-17). Some echinoids are quite colorful.
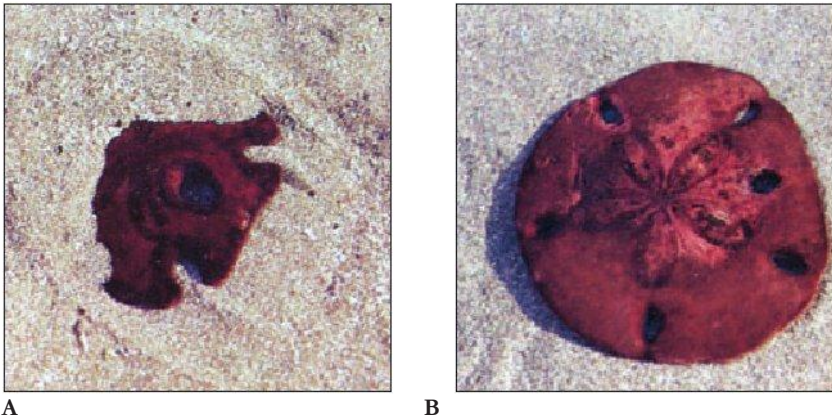
Echinoids have a wide distribution in all seas, from intertidal regions to deep oceans. Regular urchins often prefer rocky or hard bottoms, whereas sand dollars and heart urchins like to burrow into a sandy substrate. Distributed along one or both coasts of North America are common genera of regular urchins (Arbacia [Gr. *Arbak f s,* first king of Media], *Strongylocentrotus* [Gr. *strongylos,* round, compact, *kentron,* point, spine] [Figure 23-15], and *Lytechinus* [Gr. *lytos,* dissolvable, broken, *echinos,* sea urchin]) and sand dollars (Dendraster [Gr. *dendron,* tree, stick, *asteros,* star] and *Echinarachnius* [Gr. *echinos,* sea urchin, *arachn f,* spider]). The West Indies-Florida region is rich in echinoderms, including echinoids, of which *Diadema* (Gr. *diade|,* to bind around), with its long, needle-sharp spines, is a notable example (Figure 23-16D).
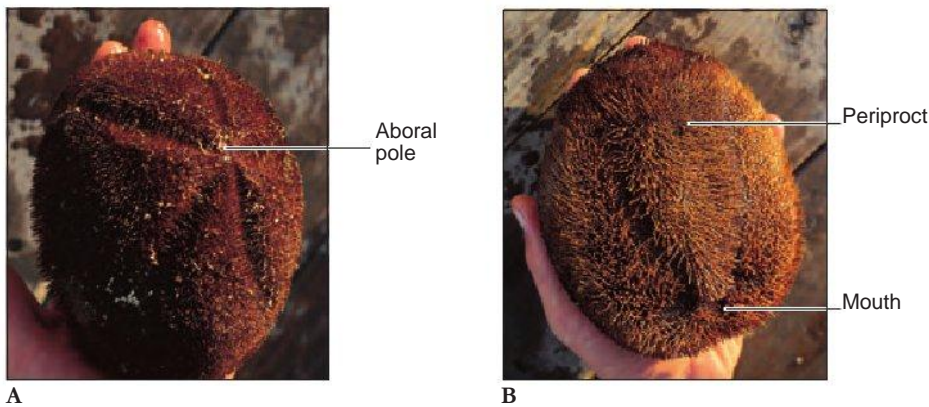
Form and Function

The echinoid test is a compact skeleton of 10 double rows of plates that bear movable, stiff spines (Figure 23-19). The plates are sutured firmly. The five pairs of ambulacral rows are homologous to the five arms of sea stars and have pores (Figure 23-19B) through which long tube feet extend. The plates bear small tubercles on which the round ends of the spines articulate as ball-and-socket joints. Spines are moved by small muscles around the bases.

There are several kinds of pedicellariae, the most common of which are three jawed and are mounted on long stalks (Figure 23-4D and E). Pedicellariae help keep the body clean, especially by preventing marine larvae from settling on the body surface. Pedicellariae of many species bear poison glands, and the toxin paralyzes small prey.

Figure 23-17

Two sand dollar species. **A,** *Encope grandis* as normally found burrowing near the surface on a sandy bottom. **B,** Removed from the sand. The short spines and petaloids on the aboral surface of this *Encope micropora* are easily seen.

Figure 23-18

An irregular echinoid *Meoma,* one of the largest heart urchins (test up to 18 cm). *Meoma* occurs in the West Indies and from the Gulf of California to the Galápagos Islands. **A,** Aboral view. Anterior ambulacral area is not modified as a petaloid in the heart urchins, although it is in the sand dollars. **B,** Oral view. Note curved mouth at anterior end and periproct at posterior end.

Diadema antillarum is not nearly as prominent as it once was. In January 1983, an epidemic swept through the Caribbean and along the Florida Keys. Its cause has never been determined, but it decimated the *Diadema* population, leaving less than 5% of the original numbers. Other species of sea urchins were unaffected. However, various types of algae, formerly grazed heavily by the *Diadema* have increased greatly on the reefs, and *Diadema* populations have not recovered. This abundance of algae has had a disastrous effect on coral reefs around Jamaica. Herbivorous fish around that island had been chronically overharvested, and then, after the *Diadema* epidemic, there was nothing left to control algal overgrowth. Coral reefs around Jamaica have been largely destroyed.
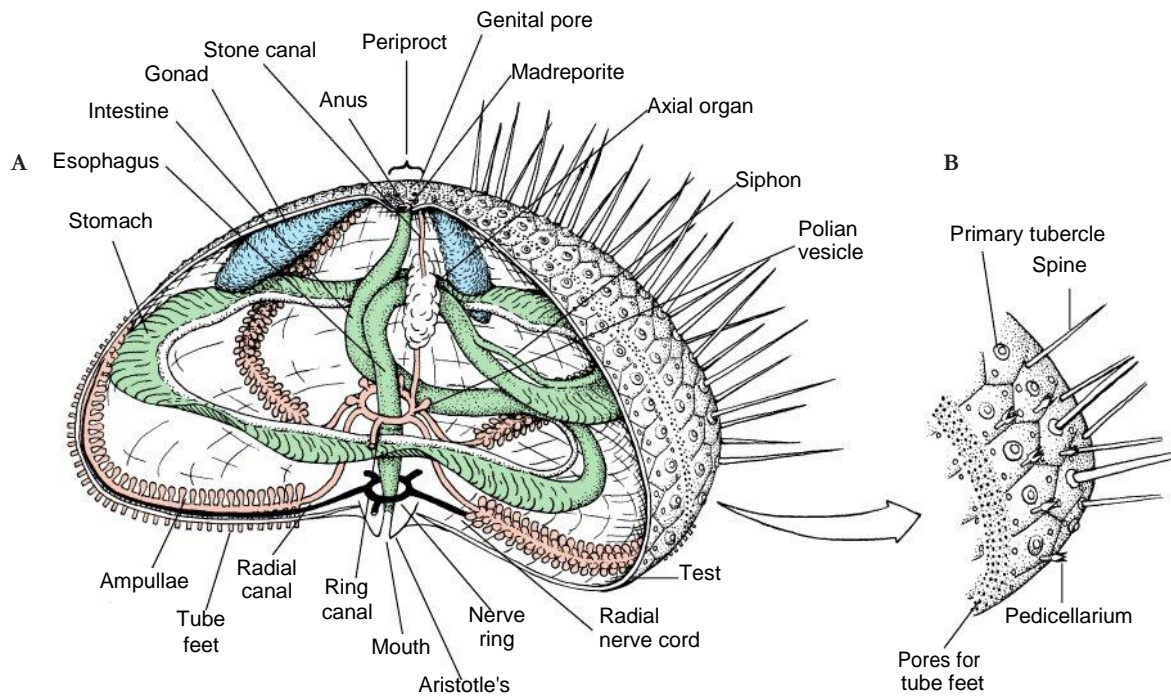
Five converging teeth surround the mouth of regular urchins. In some sea urchins branched gills (modified podia) encircle the peristome. The anus, genital pores, and madreporite are located aborally in the periproct region (Figure 23-19). Sand dollars also have teeth, and the mouth is located at about the center of the oral side, but the anus has shifted to the posterior margin or even the oral side of the disc, so that an anteroposterior axis and bilateral symmetry can be recognized. Bilateral symmetry is even more accentuated in heart urchins, with the anus near the posterior on the oral side and the mouth moved away from the oral pole toward the anterior (Figure 23-18).

Inside the test (Figure 23-19) are the coiled digestive system and a complex chewing mechanism (in regular urchins and in sand dollars), called **Aristotle's lantern** (Figure 23-20), to which the teeth are attached. A ciliated **siphon** connects the esophagus to the intestine and enables water to bypass the stomach to concentrate food for digestion in the intestine. Sea urchins eat algae and other organic material, which they graze with their teeth. Sand dollars have short club-shaped spines that move the sand and its organic contents over the aboral surface and down the sides. Fine food particles drop between the spines, and ciliated tracts on the oral side carry the particles to the mouth.
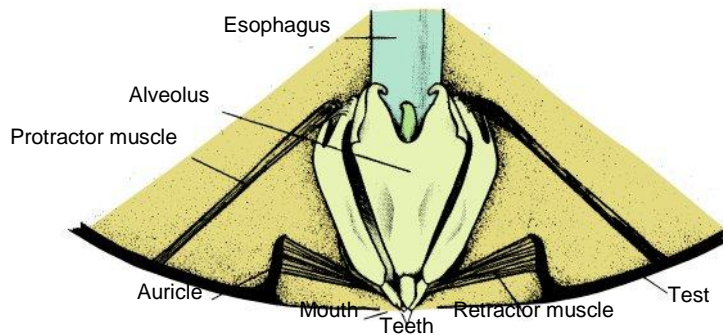
Hemal and nervous systems are basically similar to those of asteroids. Ambulacral grooves are closed, and radial canals of the water-vascular system run just beneath the test, one in each of the ambulacral radii (Figure 23-19). Ampullae for the podia are within the test, and each ampulla usually communicates with its podium by *two* canals through pores in the ambulacral plate; consequently, such pores in the plates are in pairs. Peristomial gills, where present, are of little or no importance in respiratory gas exchange, this function being carried out principally by the other podia. In irregular urchins respiratory podia are thin walled, flattened, or lobulate and are arranged in ambulacral fields called **petaloids** on the aboral surface. Irregular urchins also have short, suckered, single-pored podia in the ambulacral and sometimes interambulacral areas; these podia function in food handling.

Sexes are separate, and both eggs and sperm are shed into the sea for external fertilization. Some, such as certain pencil urchins, brood their young in depressions between the spines. **Echinopluteus larvae** (Figure 23-10D) of nonbrooding echinoids may live a planktonic existence for several months and then metamorphose quickly into young urchins.

Figure 23-19

A, Internal structure of a sea urchin; water-vascular system in tan. **B,** Detail of portion of endoskeleton.

Figure 23-20

Aristotle's lantern, a complex mechanism used by the sea urchin for masticating its food. Five pairs of retractor muscles draw the lantern and teeth up into the test; five pairs of protractors push the lantern down and expose the teeth. Other muscles produce a variety of movements. Only major skeletal parts and muscles are shown in this diagram.

Class Holothuroidea

In a phylum characterized by odd animals, class Holothuroidea (sea cucumbers) contains members that both structurally and physiologically are among the strangest. These animals have a remarkable resemblance to the vegetable after which they are named (Figure 23-21). Compared with other echinoderms, holothurians are greatly elongated in the oral-aboral axis, and ossicles are much reduced in most, so that the animals are soft bodied. Some species crawl on the surface of the sea bottom, others are found beneath rocks, and some are burrowers.

Common species along the east coast of North America are *Cucumaria frondosa* (L. *cucumis,* cucumber), *Sclerodactyla briareus* (Gr. *skleros,* hard, *daktylos,* finger) (Figure 23-23), and the translucent, burrowing *Leptosynapta* (Gr. *leptos,* slender, *synapsis,*

joining together). Along the Pacific coast there are several species of *Cucumaria* (Figure 23-21C) and the striking reddish brown *Parastichopus* (Gr. *para,* beside, *stichos,* line or row, *pous, podos,* foot) (Figure 23-21A), with very large papillae.

Form and Function

The body wall is usually leathery, with tiny ossicles embedded in it (Figure 23-22), although a few species have large ossicles forming a dermal armor (Figure 23-21B). Because of the elongate body form of sea cucumbers, they characteristically lie on one side. In some species locomotor tube feet are equally distributed to the five ambulacral areas (Figure 23-21C) or all over the body, but most have well-developed tube feet only in the ambulacra normally applied to the substratum (Figure 23-21A and B). Thus a secondary bilaterality is present, albeit of quite different origin from that of irregular urchins. The side applied to the substratum has three ambulacra and is called the **sole;** tube feet in the dorsal ambulacral areas, if present, are
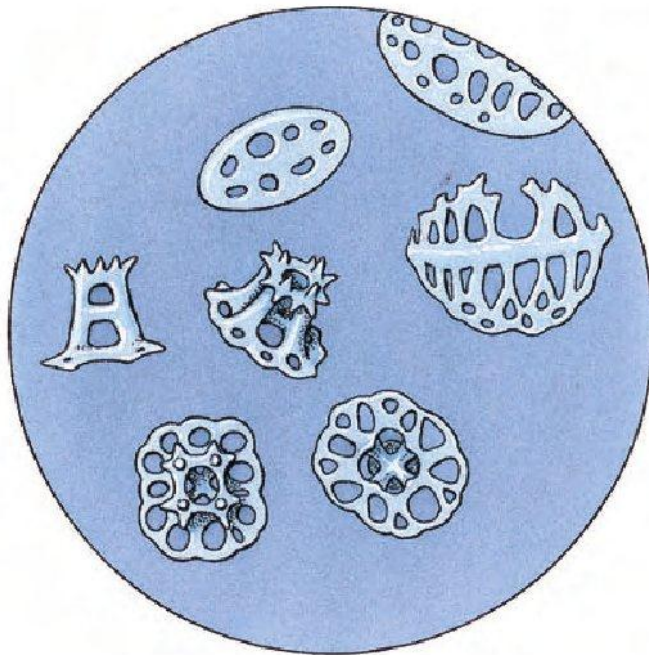
A   **B**   **C**

Figure 23-21
Sea cucumbers (class Holothuroidea). **A,** Common along the Pacific coast of North America, *Parastichopus californicus* grows to 50 cm in length. Its tube feet on the dorsal side are reduced to papillae and warts. **B, In sharp** contrast to most sea cucumbers, the surface ossicles of *Psolus chitonoides* are developed into a platelike armor. The ventral surface is a flat, soft, creeping sole, and the mouth (surrounded by tentacles) and anus are turned dorsally. **C,** Tube feet are found in all ambulacral areas of *Cucumaria miniata* but are better developed on its ventral side, shown here.

Figure 23-22
Ossicles of sea cucumbers are usually microscopic bodies buried in the leathery dermis. They can be extracted from the tissue with commercial bleach and are important taxonomic characteristics. The ossicles shown here, called tables, buttons, and plates, are from the sea cucumber *Holothuria difficilis.* They illustrate the meshwork (stereom) structure observed in ossicles of all echinoderms at some stage in their development (250).

ure 23-23). A **respiratory tree** composed of two long, many-branched tubes also empties into the cloaca, which pumps seawater into it. The respiratory tree serves for both respiration and excretion and is not present in any other group of living echinoderms. Gas exchange also occurs through the skin and tube feet.
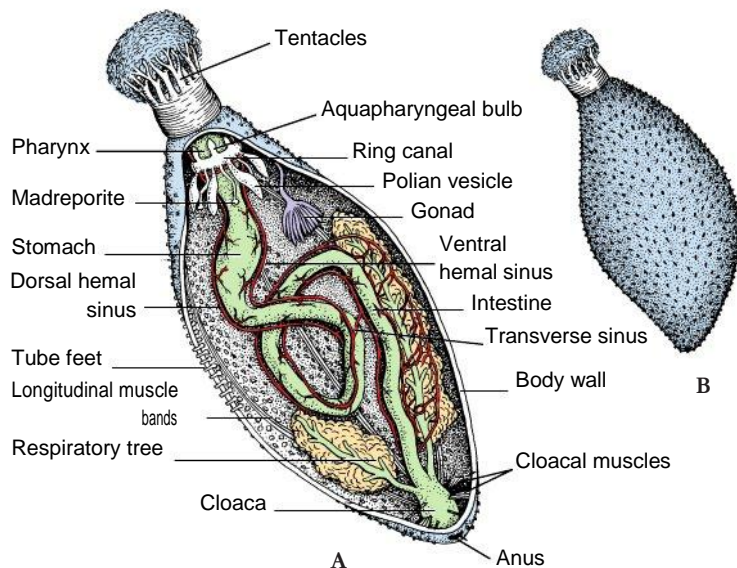
The hemal system is more well developed in holothurians than in other echinoderms. The water-vascular system is peculiar in that the madreporite lies free in the coelom.

Sexes are usually separate, but some holothurians are hermaphroditic. Among echinoderms, only sea cucumbers have a single gonad, and this is considered a primitive character. The gonad is usually in the form of one or two clusters of tubules that join at the gonoduct. Fertilization is external, and the free-swimming larva is called an **auricularia** (Figure 23-10E). Some species brood the young either inside the body or somewhere on the body surface.

Biology

Sea cucumbers are sluggish, moving partly by means of their ventral tube feet and partly by waves of contraction in the muscular body wall. More sedentary species trap suspended food particles in the mucus of their outstretched oral tentacles or pick up particles from the surrounding bottom.

usually without suckers and may be modified as sensory papillae. All tube feet, except oral tentacles, may be absent in burrowing forms.

The oral tentacles are 10 to 30 retractile, modified tube feet around the mouth. The body wall contains circular and longitudinal muscles along the ambulacra.

The coelomic cavity is spacious and fluid filled and has many coelomocytes. Because of the reduction in dermal ossicles, they no longer function as an endoskeleton, and the fluid-filled coelom now serves as a hydrostatic skeleton.

The digestive system empties posteriorly into a muscular **cloaca** (Fig-

Tentacles

Aquapharyngeal bulb

Pharynx

Ring canal

Polian vesicle

Madreporite

Gonad

Stomach

Ventral hemal sinus

Dorsal hemal sinus

Intestine

Transverse sinus

Tube feet

Body wall

Longitudinal muscle bands

Respiratory tree

Cloacal muscles

Cloaca

Anus

A

B

Figure 23-23
Anatomy of the sea cucumber *Sclerodactyla.* **A,** Internal. **B,** External. *Red,* hemal system.

A

B

C

Figure 23-24
A, *Eupentacta quinquesemita* extends its tentacles to collect particulate matter in the water, then puts them one by one into its mouth and cleans the food from them. **B,** Moplike tentacles of *Parastichopus californicus* are used for deposit feeding on the bottom. **C,** *Bohadschia argus* expels its cuvierian tubules, modified parts of its respiratory tree, when it is disturbed. These sticky strands, containing a toxin, discourage potential predators.

They then stuff their tentacles into the pharynx, one by one, sucking off the food material (Figure 23-24A). Others crawl along, grazing the bottom with their tentacles (Figure 23-24B).

Sea cucumbers have a peculiar power of what appears to be self-mutilation but may be a mode of defense. When irritated or when subjected to unfavorable conditions, many species can cast out a part of their viscera by a strong muscular contraction that may either rupture the body wall or evert its contents through the anus. Lost parts are soon regenerated. Certain species have organs of Cuvier (cuvierian tubules), which are attached to the posterior part of the respiratory tree and can be expelled in the direction of an enemy (Figure 23-24C). These tubules become long and sticky after expulsion, and some contain toxins.
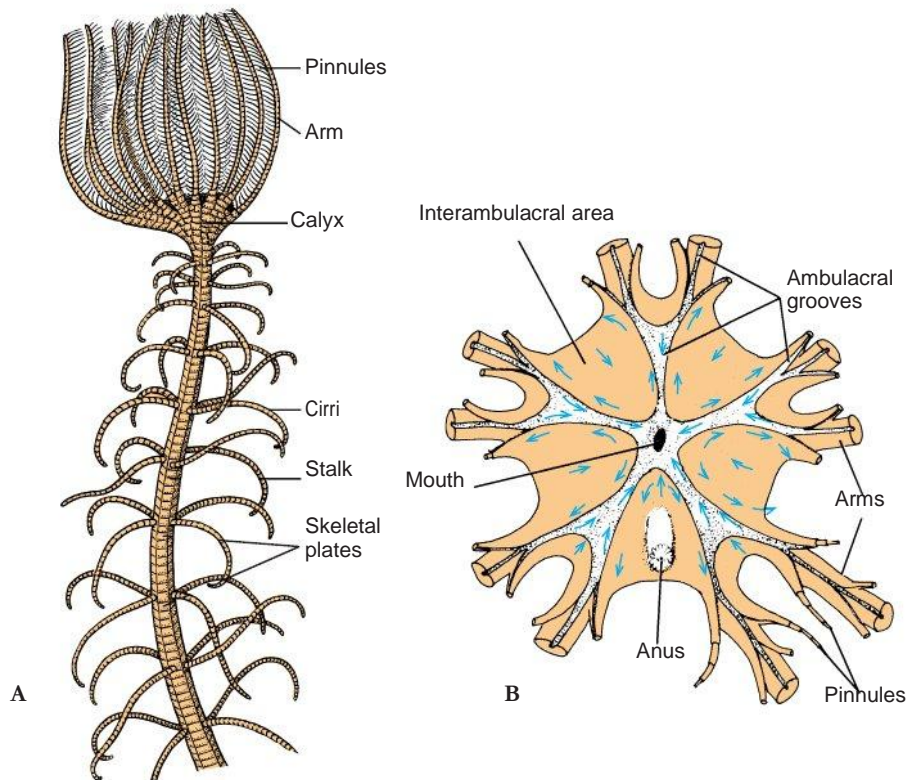
There is an interesting commensal relationship between some sea cucumbers and a small fish, *Carapus,* that uses the cloaca and respiratory tree of the sea cucumber as shelter.

Class Crinoidea

Crinoids include sea lilies and feather stars. They have several primitive characters. As fossil records reveal, crinoids were once far more numerous than they are now. They differ from other echinoderms by being attached during a substantial part of their lives. Sea lilies have a flower-shaped body that is placed at the tip of an attached stalk (Figure 23-25). Feather stars have long, many-branched arms, and adults are free moving, though they may remain in the same spot for long periods (Figure 23-26). During metamorphosis feather stars become sessile and stalked, but after several months they detach and become free moving. Many crinoids are deep-water forms, but feather stars may inhabit shallow waters, especially in the Indo-Pacific and West-Indian–Caribbean regions, where the largest numbers of species are found.

Form and Function

The body disc, or **calyx,** is covered with a leathery skin **(tegmen)** containing calcareous plates. The epidermis is poorly developed. Five flexible arms branch to form many more arms, each with many lateral **pinnules** arranged like barbs on a feather (Figure 23-25). Calyx and arms together are called the **crown.** Sessile forms have a long, jointed **stalk** attached to the aboral

Figure 23-25
Crinoid structure. **A,** Sea lily (stalked crinoid) with portion of stalk. Modern crinoid stalks rarely exceed 60 cm, but fossil forms were as much as 20 m long. **B,** Oral view of calyx of the crinoid *Antedon,* showing direction of ciliary food currents. Ambulacral grooves with podia extend from mouth along arms and branching pinnules. Food particles touching podia are tossed into ambulacral grooves and carried, tangled in mucus, by strong ciliary currents toward mouth. Particles falling on interambulacral areas are carried by cilia first toward mouth and then outward and finally dropped off the edge, thus keeping the oral disc clean.

Figure 23-26
Comantheria briareus are crinoids found on Pacific coral reefs. They extend their arms into the water to catch food particles both during the day and at night.

side of the body. This stalk is composed of plates, appears jointed, and may bear **cirri.** Madreporite, spines, and pedicellariae are absent.

The upper (oral) surface bears the mouth, which opens into a short esophagus, from which the long intestine with diverticula proceeds aborally for a distance and then makes a complete turn to the **anus,** which may be on a raised cone (Figure 23-25B). With the aid of tube feet and mucous nets, crinoids feed on small organisms that are caught in their ambulacral grooves. **Ambulacral grooves** are open and ciliated and serve to carry food to the mouth (Figure 23-25B). Tube feet in the form of tentacles are also found in the grooves.

The water-vascular system has the basic echinoderm plan. The nervous system has an oral ring and a radial nerve that runs to each arm. The aboral or entoneural system is more highly developed in crinoids than in most other echinoderms. Sense organs are scanty and primitive.

Sexes are separate. Gonads are simply masses of cells in the genital cavity of the arms and pinnules. Gametes escape without ducts through a rupture in the pinnule wall. Brooding occurs in some forms. **Doliolaria** larvae (Figure 23-10F) are free swimming for a time before they become attached and metamorphose. Most living crinoids are from 15 to 30 cm long, but some fossil species had stalks 20 m in length.

Class Concentricycloidea

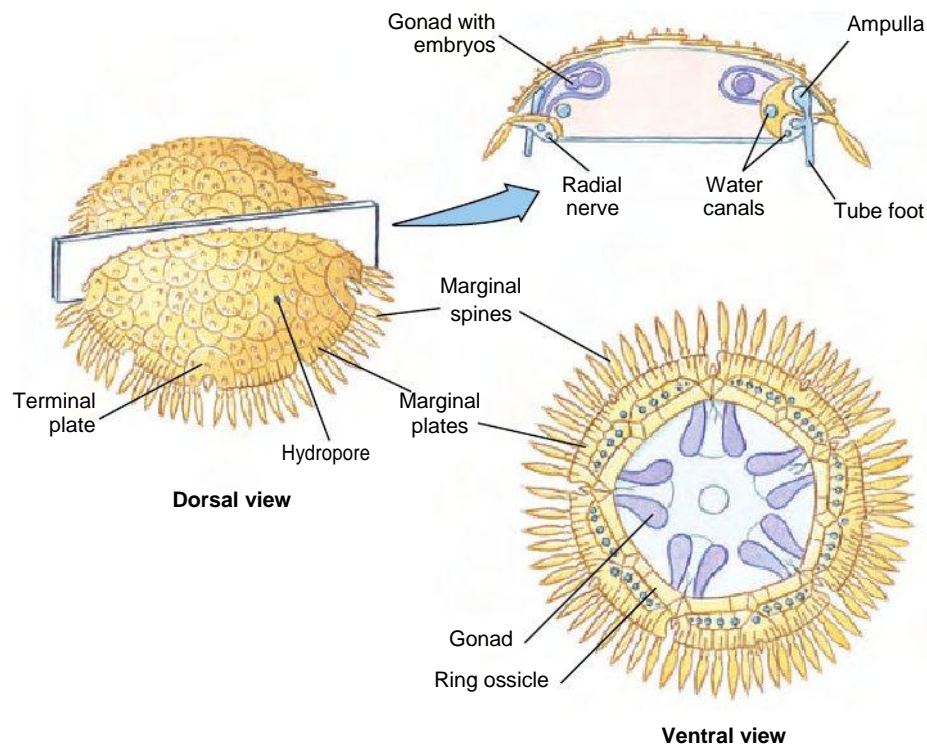Strange little (less than 1 cm diameter), disc-shaped animals (Figure 23-27) were discovered in water over 1000 m deep off New Zealand. Sometimes called sea daisies, they are the most recently described (1986) class of echinoderms, and only two species are known so far. They are pentaradial in symmetry but have no arms. Their tube feet are located around the periphery of the disc, rather than along ambulacral areas, as in other echinoderms. Their water-vascular system includes two concentric ring canals; the outer ring may represent radial canals since podia arise from it. A hydropore, homologous to the madreporite, connects the inner ring canal to the aboral surface. One species has no digestive tract; its oral surface is covered by a membranous **velum,** by which it apparently absorbs nutrients. The other species has a shallow, saclike stomach but no intestine or anus.

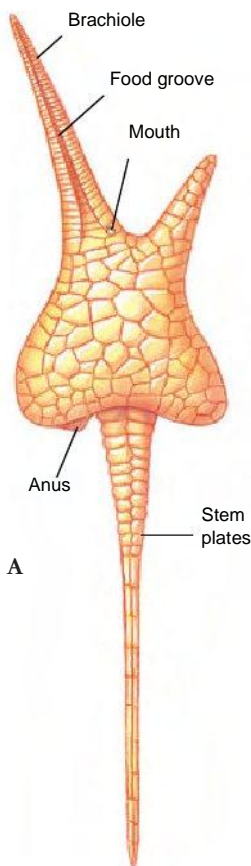## Phylogeny and Adaptive Radiation

Phylogeny

Despite the existence of an extensive fossil record, there have been numerous contesting hypotheses on echinoderm phylogeny. Based on the embryological evidence of the bilateral larvae, there can be little doubt that their ancestors were bilateral and that their coelom had three pairs of spaces (trimeric). Some investigators have held that radial symmetry arose in a free-moving echinoderm ancestor and

Gonad with embryos

Ampulla

Radial nerve

Water canals

Tube foot

Terminal plate

Hydropore

Marginal spines

Marginal plates

Dorsal view
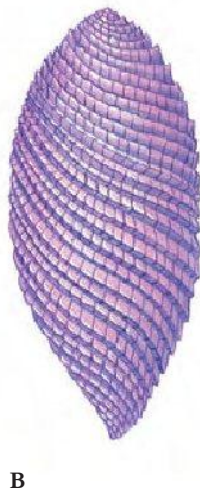
Gonad

Ring ossicle

Ventral view

Figure 23-27

Xyloplax spp. (class Concentricycloidea) are bizarre little disc-shaped echinoderms. With their podia around the margin, they are the only echinoderms not having podia distributed along ambulacral areas.

Brachiole

Food groove

Mouth

Anus

Stem plates

A

B

Figure 23-28

A, *Dendrocystites,* a carpoid (subphylum Homalozoa) with one brachiole. Brachioles are so called to distinguish them from the heavier arms of asteroids, ophiuroids and crinoids. This group bore some characters interpreted as chordate in nature. It is called Calcichordata by some investigators (p. 494).
B, *Helicoplacus,* a helicoplacoid, had three ambulacral areas and apparently a water-vascular system. It is the sister group to modern echinoderms.

that sessile groups were derived several times independently from the free-moving ancestors. However, this view does not account for the adaptive significance of radial symmetry as an adaptation for a sessile existence. The more traditional view is that the first echinoderms were sessile, became radial as an adaptation to that existence, and then gave rise to the free-moving groups. Figure 23-29 is consistent with this hypothesis. It views evolution of endoskeletal plates with stereom structure and of external ciliary grooves for feeding as early echinoderm (or pre-echinoderm) developments. The extinct carpoids (Figures 23-28A, 23-29) had stereom ossicles but were not radially symmetrical, and the status of their water-vascular system, if any, is uncertain. Some investigators regard carpoids as a separate subphylum of echinoderms (Homalozoa) and consider them closer to chordates (Calcichordata, p. 494). The fossil helicoplacoids (Figures 23-28B, 23-29) show evidence of three, true ambulacral grooves, and their mouth was on the side of the body.

Attachment to the substratum by the aboral surface would have led to radial symmetry and the origin of the Pelmatozoa. Both Cystoidea (extinct) and Crinoidea primitively were attached to the substratum by an aboral stalk. An ancestor that became free-moving and applied its oral surface to the substratum would have given rise to Eleutherozoa. Phylogeny within Eleutherozoa is controversial. Most investigators agree that echinoids and holothuroids are related and form a clade, but opinions diverge on the relationship of ophiuroids and asteroids. Figure 23-29 illustrates the view that the ophiuroids arose after the closure of ambulacral grooves, but this scheme treats evolution of five ambulacral rays (arms) in ophiuroids and asteroids as independently evolved. Alternatively, if ophiuroids and asteroids are a single clade, then closed ambulacral grooves must have evolved separately in ophiuroids and in the common ancestor of echinoids and holothuroids.

Classification of Phylum Echinodermata

There are about 6,000 living and 20,000 extinct or fossil species of Echinodermata. The traditional classification placed all free-moving forms that were oriented with oral side down in subphylum Eleutherozoa, containing most living species. The other subphylum, Pelmatozoa, contained mostly forms with stems and oral side up; most extinct classes and living Crinoidea belong to this group. Although alternative schemes have strong supporters, cladistic analysis provides evidence that the two traditional subphyla are monophyletic.* The following includes only groups with living members.

Subphylum Pelmatozoa (pel-ma to-zo a) (Gr. *pelmatos;* a stalk, *z|on,* animal). Body in form of cup or calyx, borne on aboral stalk during part or all of life; oral surface directed upward; open ambulacral grooves; madreporite absent; both mouth and anus on oral surface; several fossil classes plus living Crinoidea.

Class Crinoidea (krin-oi de-a) (Gr. *krinon,* lily; *eidos,* form; *ea,* characterized by): **sea lilies** and

*Brusca, R. C., and G. J. Brusca. 1990. Invertebrates. Sunderland, Massachusetts, Sinauer Associates; Meglitsch, P. A., and F. R. Schram. 1991. Invertebrate zoology, ed. 3. New York, Oxford University Press; and Paul, C. R. S., and A. B. Smith. 1984. Biol. Rev. **59:443–481.**

feather stars. Five arms branching at base and bearing pinnules; ciliated ambulacral grooves on oral surface with tentacle-like tube feet for food gathering; spines, madreporite, and pedicellariae absent. Examples: *Antedon, Comantheria* (Figure 23-26).

Subphylum Eleutherozoa (e-lu ther-o-zo a) (Gr. *eleutheros,* free, not bound, *z|on,* animal). Body form star-shaped, globular, discoidal, or cucumber-shaped; oral surface directed toward substratum or oral-aboral axis parallel to substratum; body with or without arms; ambulacral grooves open or closed.

Class Concentricycloidea (konsen tri-sy-kloy de-a) (L. *cum,* together, *centrum,* center [having a common center], Gr. *kyklos,* circle, *eidos,* form, *ea,* characterized by): **sea daisies.** Disc-shaped body, with marginal spines but no arms; concentrically arranged skeletal plates; ring of suckerless podia near body margin; hydropore present; gut present or absent, no anus. Example: *Xyloplax* (Figure 23-27).

Class Asteroidea (as ter-oy de-a) (Gr. *aster,* star, *eidos,* form, *ea,* characterized by): **sea stars (starfish).** Star-shaped, with arms not sharply marked off from central disc; ambulacral grooves open, with tube feet on oral side; tube feet often with suckers; anus and madreporite aboral; pedicellariae present. Examples: *Asterias, Pisaster* (p. 458).

Class Ophiuroidea (o fe-u-roy de-a) (Gr. *ophis,* snake, *oura,* tail, *eidos,* form, *ea,* characterized by): **brittle stars** and **basket stars.** Star shaped, with arms sharply marked off from central disc; ambulacral grooves closed, covered by ossicles; tube feet without suckers and not used for locomotion; pedicellariae absent; anus absent. Examples: *Ophiura* (Figure 23-11A), *Gorgonocephalus* (Figure 23-14B).

Class Echinoidea (ek i-noy de-a) (Gr. *echinos,* sea urchin, hedgehog, *eidos,* form, ea, characterized by): **sea urchins, sea biscuits,** and **sand dollars.** More or less globular or disc-shaped, with no arms; compact skeleton or test with closely fitting plates; movable spines; ambulacral grooves closed; tube feet with suckers; pedicellariae present. Examples: *Arbacia, Strongylocentrotus* (Figure 23-15), *Lytechinus, Mellita.*

Class Holothuroidea (hol o-thu-roy de-a) (Gr. *holothourion,* sea cucumber, *eidos,* form, *ea,* characterized by): **sea cucumbers.** Cucumber-shaped, with no arms; spines absent; microscopic ossicles embedded in thick muscular wall; anus present; ambulacral grooves closed; tube feet with suckers; circumoral tentacles (modified tube feet); pedicellariae absent; madreporite internal. Examples: *Sclerodactyla, Parastichopus, Cucumaria* (Figure 23-21C).

Data on the Concentricycloidea are insufficient to place this group on a cladogram, although they are tentatively placed in Eleutherozoa.
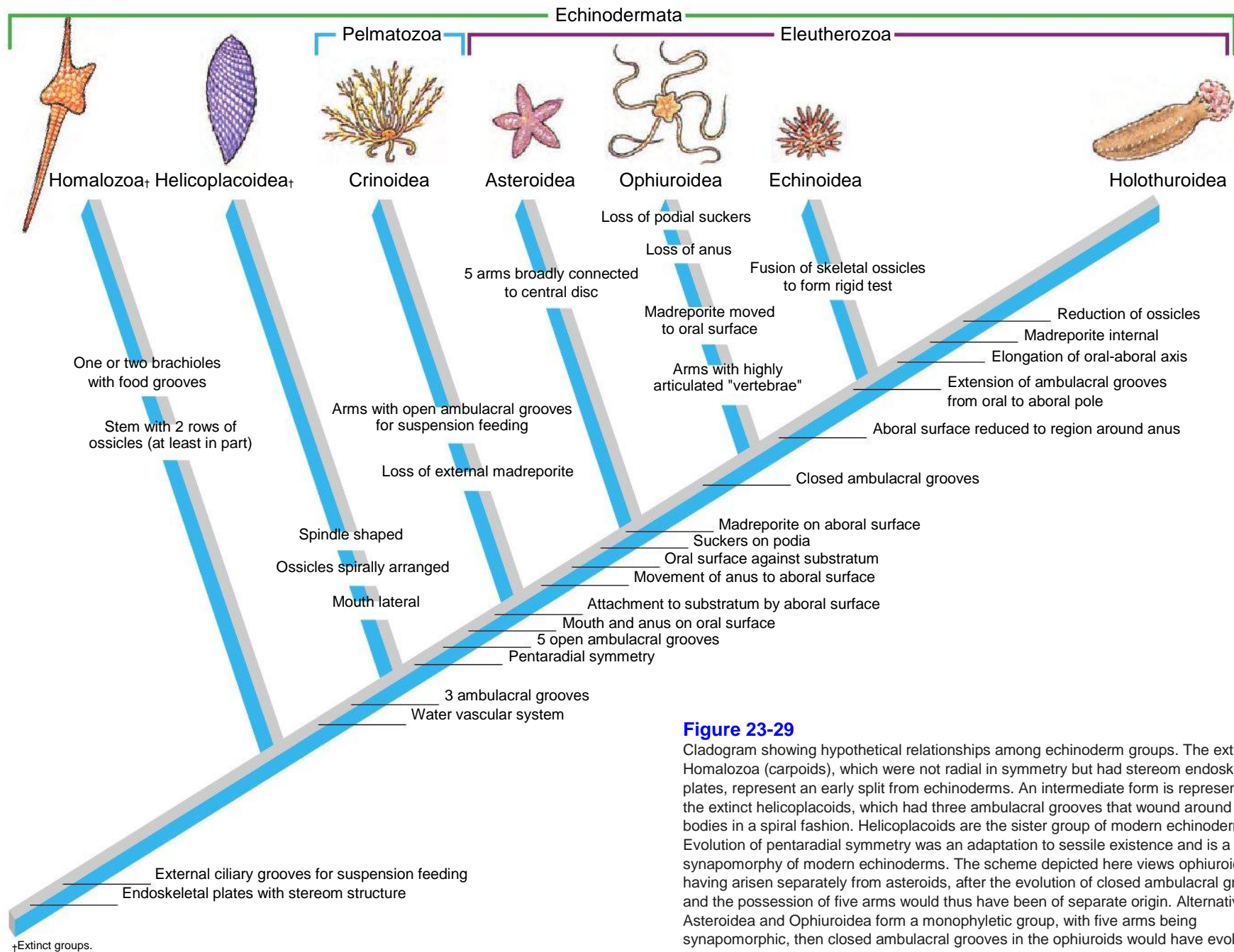
Adaptive Radiation

Radiation of echinoderms has been determined by limitations and potentials inherent in their most important characters: radial symmetry, water-vascular system, and dermal endo-skeleton. If their ancestors had a brain and specialized sense organs, these were lost in the adoption of radial symmetry. Thus it is not surprising that there are large numbers of creeping, benthic forms with filter-feeding, deposit-feeding, scavenging, and herbivorous habits, comparatively few predators, and very rare pelagic forms. In this light the relative success of asteroids as predators is impressive and probably attributable to the extent to which they have exploited the hydraulic mechanism of their tube feet.

The basic body plan of echinoderms has severely limited their evolutionary opportunities to become parasites. Indeed, the most mobile of echinoderms, the ophiuroids, which are also the ones most able to insert their bodies into small spaces, are the only group with significant numbers of commensal species.

Echinodermata

Pelmatozoa

Eleutherozoa

Homalozoa† Helicoplacoidea† Crinoidea Asteroidea Ophiuroidea Echinoidea Holothuroidea

Loss of podial suckers

Loss of anus

5 arms broadly connected
to central disc

Fusion of skeletal ossicles
to form rigid test

Madreporite moved
to oral surface

Reduction of ossicles

Madreporite internal

Elongation of oral-aboral axis

One or two brachioles
with food grooves

Arms with highly
articulated "vertebrae"

Extension of ambulacral grooves
from oral to aboral pole

Stem with 2 rows of
ossicles (at least in part)

Arms with open ambulacral grooves
for suspension feeding

Aboral surface reduced to region around anus

Loss of external madreporite

Closed ambulacral grooves

Madreporite on aboral surface
Suckers on podia
Spindle shaped
Oral surface against substratum
Ossicles spirally arranged
Movement of anus to aboral surface
Mouth lateral
Attachment to substratum by aboral surface
Mouth and anus on oral surface
5 open ambulacral grooves
Pentaradial symmetry

3 ambulacral grooves
Water vascular system

Figure 23-29
Cladogram showing hypothetical relationships among echinoderm groups. The extinct Homalozoa (carpoids), which were not radial in symmetry but had stereom endoskeletal plates, represent an early split from echinoderms. An intermediate form is represented by the extinct helicoplacoids, which had three ambulacral grooves that wound around their bodies in a spiral fashion. Helicoplacoids are the sister group of modern echinoderms. Evolution of pentaradial symmetry was an adaptation to sessile existence and is a synapomorphy of modern echinoderms. The scheme depicted here views ophiuroids as having arisen separately from asteroids, after the evolution of closed ambulacral grooves, and the possession of five arms would thus have been of separate origin. Alternatively, if Asteroidea and Ophiuroidea form a monophyletic group, with five arms being synapomorphic, then closed ambulacral grooves in the ophiuroids would have evolved separately from that character in echinoids and holothuroids

External ciliary grooves for suspension feeding
Endoskeletal plates with stereom structure

†Extinct groups.

Summary

Phylum Echinodermata shows the characteristics of the Deuterostomia division of the animal kingdom. They are an important marine group sharply distinguished from other phyla of animals. They have radial symmetry but were derived from bilateral ancestors.

Sea stars (class Asteroidea) can be used to illustrate echinoderms. Sea stars usually have five arms, which merge gradually with a central disc. Like other echinoderms, they have no head and few specialized sensory organs. The mouth is directed toward the substratum. They have stereom dermal ossicles, respiratory papulae, and open ambulacral grooves. Many sea stars have pedicellariae. Their water-vascular system is an elaborate hydraulic system derived embryonically from one of their coelomic compartments. Along the ambulacral areas, branches of the water-vascular system (tube feet) are important in locomotion, food gathering, respiration, and excretion. Many sea stars are predators, whereas others feed on small particles. Sexes are separate, and reproductive systems are very simple. The bilateral, free-swimming larva becomes attached, transforms to a radial juvenile, then detaches and becomes a motile sea star.

Arms of brittle stars (class Ophiuroidea) are slender and sharply set off from the central disc. Ophiuroids have no pedicellariae or ampullae and their ambulacral grooves are closed. Their tube feet have no suckers, and their madreporite is on the oral side. They crawl by means of arm movements, and their tube feet function in food gathering.

Dermal ossicles of sea urchins (class Echinoidea) are closely fitting plates, the body is compact, and there are no arms. Ambulacral areas are closed and extend around their body toward the aboral pole. Sea urchins move by means of tube feet or by their spines. Some urchins (sand dollars and heart urchins) have returned to adult bilateral symmetry.

Dermal ossicles in sea cucumbers (class Holothuroidea) are very small; therefore the body wall is soft. Their ambulacral areas also are closed and extend toward the aboral pole. Holothuroids are greatly elongated in the oral-aboral axis and lie on their side. Because certain of the ambulacral areas are characteristically against the substratum, sea cucumbers have also undergone some return to bilateral symmetry. The tube feet around the mouth are modified into tentacles, with which they feed. They have an internal respiratory tree, and the madreporite hangs free in the coelom.

Sea lilies and feather stars (class Crinoidea) are the only group of living echinoderms, other than asteroids, with open ambulacral grooves. They are mucociliary particle feeders and lie with their oral side up.

Sea daisies (class Concentricycloidea) are a newly discovered class of very small echinoderms that are circular in shape, have marginal tube feet, and two concentric ring canals in their water-vascular system.

Ancestors of echinoderms were bilaterally symmetrical, and they probably evolved through a sessile stage that became radially symmetrical and then gave rise to free-moving forms.

Review Questions

1. What constellation of characteristics is possessed by echinoderms and is found in no other phylum?
2. How do we know that echinoderms were derived from an ancestor with bilateral symmetry?
3. Distinguish the following groups of echinoderms from each other: Crinoidea, Asteroidea, Ophiuroidea, Echinoidea, Holothuroidea, Concentricycloidea.
4. What is an ambulacrum, and what is the difference between open and closed ambulacral grooves?
5. Trace or make a rough copy of Figure 23-3B without labels; then from memory label the parts of the water-vascular system of sea stars.
6. Briefly explain the mechanism of action of a sea star's tube foot.
7. What structures are involved in the following functions in sea stars? Briefly describe the action of each: respiration, feeding and digestion, excretion, reproduction.
8. Compare the structures and functions in question 7 as they are found in brittle stars, sea urchins, sea cucumbers, and crinoids.
9. Briefly describe development in sea stars, including metamorphosis.
10. Match the groups in the left column with *all* correct answers in the right column.

___ Crinoidea	a. Closed ambulacral grooves
___ Asteroidea	b. Oral surface generally upward
___ Ophiuroidea	c. With arms
___ Echinoidea	d. Without arms
	e. Approximately globular or disc-shaped
___ Holothuroidea	f. Elongated in oral-aboral axis
___ Concentricycloidea	g. With pedicellariae
	h. Madreporite internal
	i. Madreporite on oral plate

11. Define the following: pedicellariae, madreporite, respiratory tree, Aristotle's lantern.
12. What evidence suggests that ancestral echinoderms were sessile?
13. Give four examples of how echinoderms are important to humans.
14. What is a major difference in the function of the coelom in holothurians compared with other echinoderms?
15. Describe a reason for the hypothesis that the ancestor of eleutherozoan groups was a radial, sessile organism.

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Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

Animal Diversity Web, University of Michigan. Phylum Echinodermata. Information about echinoderms, with links to various groups of echinoderms. Nice pictures: check out the magnificent urchin, *Astropyga magnifica.* It's obvious why it was so named!

Introduction to the Echinoderms. University of California at Berkeley Museum of Paleontology site provides information on the echinoderm fossil record, life histories, systematics, and morphology. It also provides a great number of links to sites that focus on each of the echinoderm classes.

The CAS Echinoderm Webpage. Information on echinoderm taxonomy and on the echinoderm collection of the California Academy of Science. It also provides links to other echinoderm sites.

The Echinoderm Newsletter. This newsletter, prepared by the National Museum of Natural History, provides information on conferences and publications on echinoderms, and gives addresses of biologists studying echinoderms.

Echinodermata. Arizona's Tree of Life Web Page. Pictures, characteristics, phylogenetic relationships, references on echinoderms.

Phylum Echinodermata, from the University of Minnesota.

· Dissection of a Starfish.

Starfish, External and Internal Anatomy.

Echinoderms. Keys to Marine Invertebrates of the Woods Hole Region. Descriptive information, definition of terminology, and keys to the echinoderms of the Woods Hole Region.

Echinoderms, University of Minnesota. Information about echinoderms, and a link to the sea star dissection home page.

OLC
Student
Center
Website

Chaetognaths and Hemichordates

Phylum Chaetognatha
Phylum Hemichordata

An enteropneust hemichordate.

Part Chordates

In the mid-nineteenth century, with interest in the origin of the chordates running high, a group of wormlike marine invertebrates of unknown relationship began to attract attention with their chordatelike characteristics. In 1885 W. Bateson named them Hemichordata and forcefully argued that these organisms should be included in phylum Chordata. Bateson pointed to several hemichordate structures that he believed were homologous with comparable features in chordates: a dorsal nerve cord, gill slits, and, most importantly, a sac-like evagination of the mouth region that he interpreted as a notochord. The notochord, a rodlike, supportive structure lying dorsal to the gut of early growth stages of all chordates, is a key distinguishing feature of the phylum Chordata. If the hemichordates possessed a notochord—even half a notochord—they had to be chordates.

Unfortunately, the structure that Bateson interpreted as a notochord neither looks like a notochord nor develops like a notochord. These and other problems with giving the hemichordates membership in the chordate club were noted in the 1930s, but by this time the concept had become firmly established in textbooks and began to assume a life of its own. Some zoologists and texts doggedly continued to assign subphylum Hemichordata to phylum Chordata for 25 or more years. Eventually most zoologists agreed that hemichordates should be viewed as a distinct phylum of "lesser" deuterostomes. Bateson's name—Hemichordata—has stuck, however, and oddly enough seems appropriate for a group of animals that, although lacking a notochord, does bear certain characters in common with true chordates. As the likely sister group of chordates, hemichordates are indeed half (or part) chordates. I

Deuterostomes include, along with Echinodermata two other phyla: Hemichordata and Chordata. Two chordate subphyla—Urochordata and Cephalochordata—are also invertebrate groups. Phylum Chaetognatha traditionally has been included among deuterostomes, but this arrangement is not supported by recent molecular evidence.* Chaetognaths do bear a number of deuterostome characters, however, and we will continue to include them in this chapter for the present. These phyla have enterocoelous development of the coelom and some form of radial cleavage.

Phylum Chaetognatha

A common name for chaetognaths is arrowworms. They are all marine animals and are highly specialized for their planktonic existence. Their relationship to other groups is obscure, although embryological characters indicate deuterostome affinities.

The name Chaetognatha (ketog na-tha) (Gr. *chaitē̄,* long flowing hair, *gnathos,* jaw) refers to the sickle-shaped bristles on each side of the mouth. This is not a large group, for only some 65 species are known. Their small, straight bodies resemble miniature torpedoes, or darts, ranging from 2.5 to 10 cm in length.

Arrowworms are all adapted for a planktonic existence, except for *Spadella (Gr. spadix,* palm frond, *ella,* dim. suffix), a benthic genus. They usually swim to the surface at night and descend during the day. Much of the time they drift passively, but they can dart forward in swift spurts, using the caudal fin and longitudinal muscles— a fact that no doubt contributes to their success as planktonic predators. Horizontal fins bordering the trunk are used in flotation rather than in active swimming.

*Telford, M. J., and P. W. H. Holland. 1993. *Mol. Biol. Evol. 10:660–676;* Wada, H., and N. Satoh. 1994. *Proc. Natl. Acad. Sci.* **91:1801–1804.**

Figure 24-1
Arrowworms. **A,** Internal structure of *Sagitta.* **B,** Scanning electron micrograph of a juvenile arrowworm, *Flaccisagitta hexaptera* (35 mm length) eating a larval fish.

Form and Function

The body of an arrowworm is unsegmented and includes a head, trunk, and postanal tail (Figure 24-1A). On the underside of the head is a large vestibule leading to the mouth. The vestibule contains teeth and is flanked on both sides by curved chitinous spines used in seizing prey. A pair of eyes is on the dorsal side. A peculiar hood formed from a fold of the neck can be drawn forward over the head and spines. When the animal captures prey, it retracts the hood, and the teeth and raptorial spines spread apart and then snap shut with startling speed. Arrowworms are voracious feeders, living on planktonic forms, especially copepods, and even small fish (Figure 24-1B). When they are abundant, as they often are, they may have a substantial ecological impact. They are nearly transparent, a characteristic of adaptive value in their role as planktonic predators.

A thin cuticle covers the body, and the epidermis is single layered except along the sides of the body, where it is stratified in a thick layer. These are the only invertebrates with a many-layered epidermis.

Arrowworms have a complete digestive system, a well-developed coelom, and a nervous system with a nerve ring containing large dorsal and ventral ganglia and a number of lateral ganglia. Sense organs include eyes, sensory bristles, and a unique U-shaped ciliary loop that extends over the neck from the back of the head. The ciliary loop may detect water currents or may be chemosensory. However, vascular, respiratory, and excretory systems are entirely lacking.

Arrowworms are hermaphroditic with either cross- or self-fertilization. Eggs of *Sagitta* (L. arrow) bear a coat of jelly and are planktonic. Eggs of other arrowworms may be attached to the body and carried about for a time. Juveniles develop directly without

Figure 24-2
Acorn worm *Saccoglossus* (Hemichordata, class Enteropneusta). **A,** External lateral view. **B,** Longitudinal section through anterior end.

metamorphosis. Chaetognath embryogenesis differs from that of typical deuterostomes in that the coelom is formed by a backward extension from the archenteron rather than by pinched-off coelomic sacs. There is no true peritoneum lining the coelom. Cleavage is radial, complete, and equal.

A common arrowworm is *Sagitta* (Figure 24-1A).

Phylum Hemichordata

Hemichordata (hem i-kor-da ta) (Gr. *hemi,* half, *chorda,* string, cord) are marine animals that were formerly considered a subphylum of chordates, based on their possession of gill slits and a rudimentary notochord. However, the so-called hemichordate notochord is really a buccal diverticulum (called a stomochord, meaning "mouth-cord") and not homologous

with the chordate notochord, so hemichordates are given the rank of a separate phylum.

Hemichordates are vermiform bottom dwellers, living usually in shallow waters. Some colonial species live in secreted tubes. Most are sedentary or sessile. Their distribution is almost cosmopolitan, but their secretive habits and fragile bodies make collecting them difficult.

Members of class Enteropneusta (Gr. *enteron,* intestine, *pneustikos,* of, or for, breathing) (acorn worms) range from 20 mm to 2.5 m in length. Members of class Pterobranchia (Gr. *pteron,* wing, *branchia,* gills) are smaller, usually 1 to 12 mm, not including the stalk. About 70 species of enteropneusts and two small genera of pterobranchs are recognized.

Hemichordates have the typical tricoelomate structure of deuterostomes.
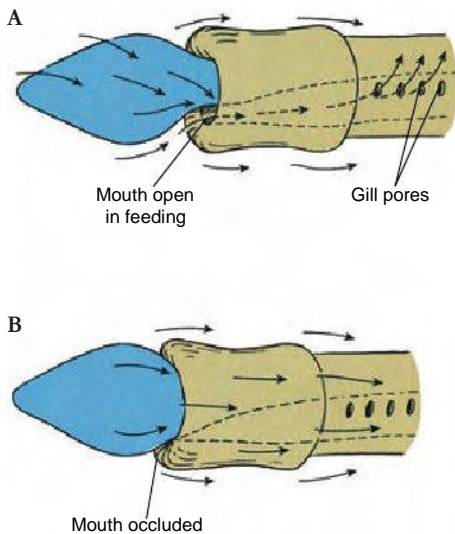
Class Enteropneusta

Enteropneusts, or acorn worms, are sluggish, wormlike animals that live in burrows or under stones, usually in mud or sand flats of intertidal zones. *Balanoglossus* (Gr. *balanos,* acorn, *gl|ssa,* tongue) and *Saccoglossus* (Gr. *sakkos,* sac, strainer, *gl|ssa,* tongue) (Figure 24-2) are common genera.

Form and Function

The mucus-covered body is divided into a tonguelike proboscis, a short collar, and a long trunk (protosome, mesosome, and metasome).

Proboscis The proboscis is the active part of the animal. It probes about in the mud, examining its surroundings and collecting food in mucous strands on its surface. Cilia carry particles to the groove at the edge of the collar, direct

Figure 24-3
Food currents of enteropneust hemichordate. **A,** Side view of acorn worm with mouth open, showing direction of currents created by cilia on proboscis and collar. Food particles are directed toward mouth and digestive tract. Rejected particles move toward outside of collar. Water leaves through gill pores. **B,** When mouth is occluded, all particles are rejected and passed onto the collar. Nonburrowing and some burrowing hemichordates use this feeding method.

them to the mouth on the underside, and then the particles are swallowed. Large particles can be rejected by covering the mouth with the edge of the collar (Figure 24-3).

Burrow dwellers use the proboscis to excavate, thrusting it into the mud or sand and allowing cilia and mucus to move the sand backward. Or they may ingest sand or mud as they go, extracting its organic contents. They build U-shaped, mucus-lined burrows, usually with two openings 10 to 30 cm apart and with the base of the U 50 to 75 cm below the surface. They can thrust their proboscis out the front opening for feeding. Defecation at the back opening builds characteristic spiral mounds of feces that leave a telltale clue to the location of burrows.

In the posterior end of the proboscis is a small coelomic sac (protocoel) into which extends the **buccal diverticulum,** a slender, blindly ending pouch of the gut that reaches forward into the buccal region and was formerly considered a notochord. A

Characteristics of Phylum Hemichordata

1. Soft bodied; wormlike or short and compact with stalk for attachment
2. Body divided into **proboscis, collar,** and **trunk;** coelomic pouch single in proboscis, but paired in other two; **buccal diverticulum** in posterior part of proboscis
3. Enteropneusta free moving and of burrowing habits; pterobranchs sessile, mostly colonial, living in secreted tubes
4. Circulatory system of dorsal and ventral vessels and dorsal heart
5. Respiratory system of **gill slits** (few or none in pterobranchs) connecting the pharynx with outside as in chordates
6. No nephridia; a single **glomerulus** connected to blood vessels may have excretory function
7. A subepidermal nerve plexus thickened to form dorsal and ventral nerve cords, with a ring connective in the collar; **dorsal nerve cord** of collar hollow in some
8. Sexes separate in Enteropneusta, with gonads projecting into body cavity; in pterobranchs reproduction may be sexual or asexual (in some) by budding; tornaria larva in some Enteropneusta

slender canal connects the protocoel with a **proboscis pore** to the outside (Figure 24-2B). The paired coelomic cavities in the collar also open by pores. By taking in water through the pores into the coelomic sacs, the proboscis and collar can be stiffened to aid in burrowing. Contraction of the body musculature then forces the excess water out through the gill slits, reducing the hydrostatic pressure and allowing the animal to move forward.

Branchial System A row of **gill pores** is located dorsolaterally on each side of the trunk just behind the collar (Figure 24-3A). Pores open from a series of gill chambers that in turn connect with a series of **gill slits** in the sides of the pharynx. There are no gills

on the gill slits, but some respiratory gaseous exchange occurs in the vascular branchial epithelium, as well as in the body surface. Ciliary currents keep a fresh supply of water moving from the mouth through the pharynx and out the gill slits and branchial chambers to the outside.
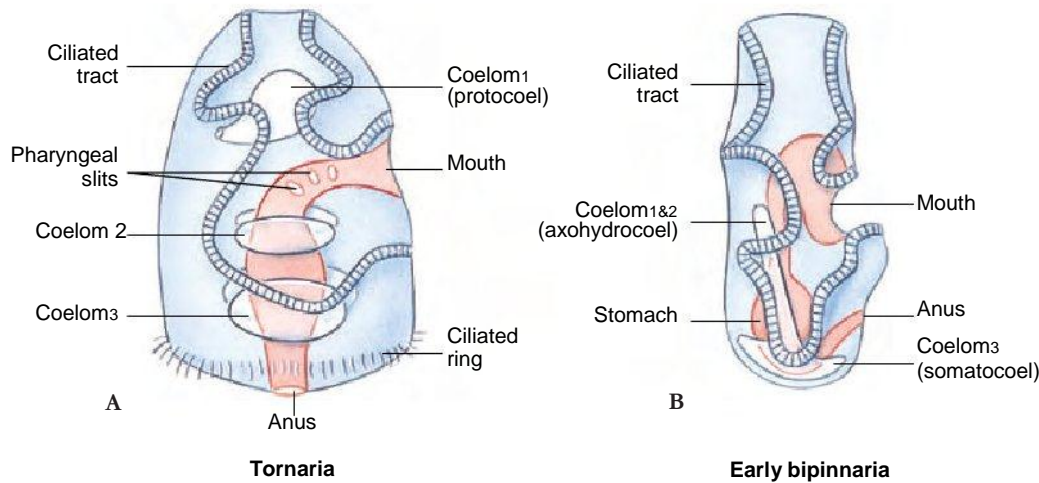
Feeding and the Digestive System
Hemichordates are largely ciliary-mucus feeders. Behind the buccal cavity lies the large pharynx containing in its dorsal part the U-shaped gill slits (Figure 24-2B). Since there are no gills, the primary function of the branchial mechanism of the pharynx is presumably food gathering. Having been caught in mucus and brought to the mouth by ciliary action on the proboscis and collar, food particles are strained from the branchial water that leaves through the gill slits. Food then passes to the ventral part of the pharynx and esophagus to the intestine, where digestion and absorption occur (Figure 24-3).

Circulatory and Excretory Systems
A middorsal vessel carries the colorless blood forward above the gut. In the collar the vessel expands into a sinus and a heart vesicle above the buccal diverticulum. Blood then enters a network of blood sinuses called the **glomerulus,** which partially surrounds these structures. The glomerulus is assumed to have an excretory function (Figure 24-2B). Blood travels posteriorly through a ventral vessel below the gut, passing through extensive sinuses to the gut and body wall.

Nervous and Sensory Systems The nervous system consists mostly of a subepithelial network, or plexus, of nerve cells and fibers to which processes of epithelial cells are attached. Thickenings of this net form dorsal and ventral nerve cords that are united posterior to the collar by a ring connective. The dorsal cord continues into the collar and furnishes many fibers to the plexus of the proboscis. The collar cord is hollow in some species and contains giant nerve cells with processes running to

Figure 24-4

Comparison of a hemichordate tornaria **(A)** to an echinoderm bipinnaria **(B).**

the nerve trunks. This nerve plexus system is quite reminiscent of that of cnidarians and echinoderms.

Sensory receptors include neurosensory cells throughout the epidermis (especially in the proboscis, a preoral ciliary organ that may be chemoreceptive) and photoreceptor cells.

Reproductive System and Development   Sexes are separate in enterop- neusts. A dorsolateral row of gonads runs along each side of the anterior part of the trunk. Fertilization is external, and in some species a ciliated **tornaria** larva develops that at certain stages is so similar to the echinoderm bipinnaria that it was once believed to be an echinoderm larva (Figure 24-4). The familiar *Saccoglossus* of American waters has direct development without a tornaria stage.
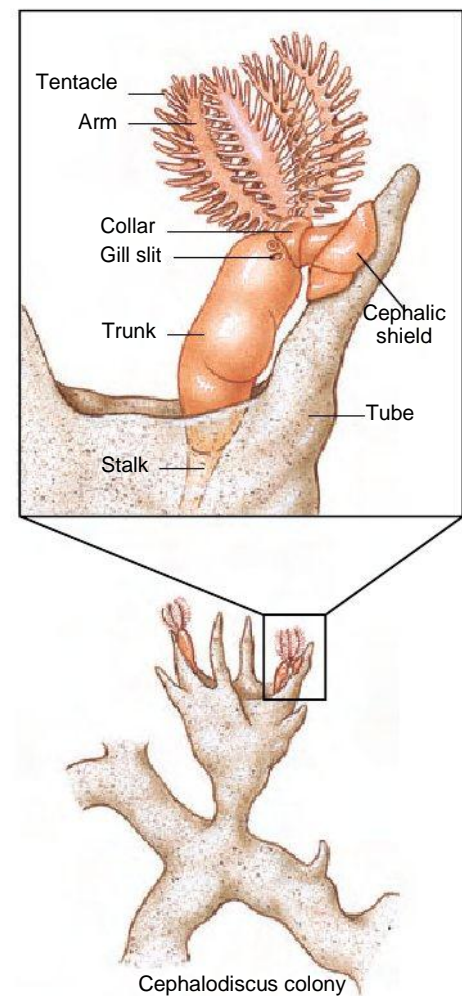
Class Pterobranchia

The basic plan of class Pterobranchia is similar to that of Enteropneusta, but certain structural differences are correlated with the sedentary life-style of pterobranchs. The first pterobranch ever reported was obtained by the famed *Challenger* expedition of 1872 to 1876. Although first placed among Polyzoa (Entoprocta and Ectoprocta), its affinities to hemichordates were later recognized. Only two genera

(Cephalodiscus and *Rhabdopleura)* are known in any detail.

Pterobranchs are small animals, usually within the range of 1 to 7 mm in length, although the stalk may be longer. Many individuals of *Cephalodiscus* (Gr. *kephalf,* head,   *diskos,* disc) (Figure 24-5) live together in collagenous tubes, which often form an anastomosing system. Zooids are not connected, however, and live independently in the tubes. Through apertures in these tubes, they extend their crown of tentacles. They are attached to the walls of the tubes by extensible stalks that can jerk the owners back into the tubes when necessary.
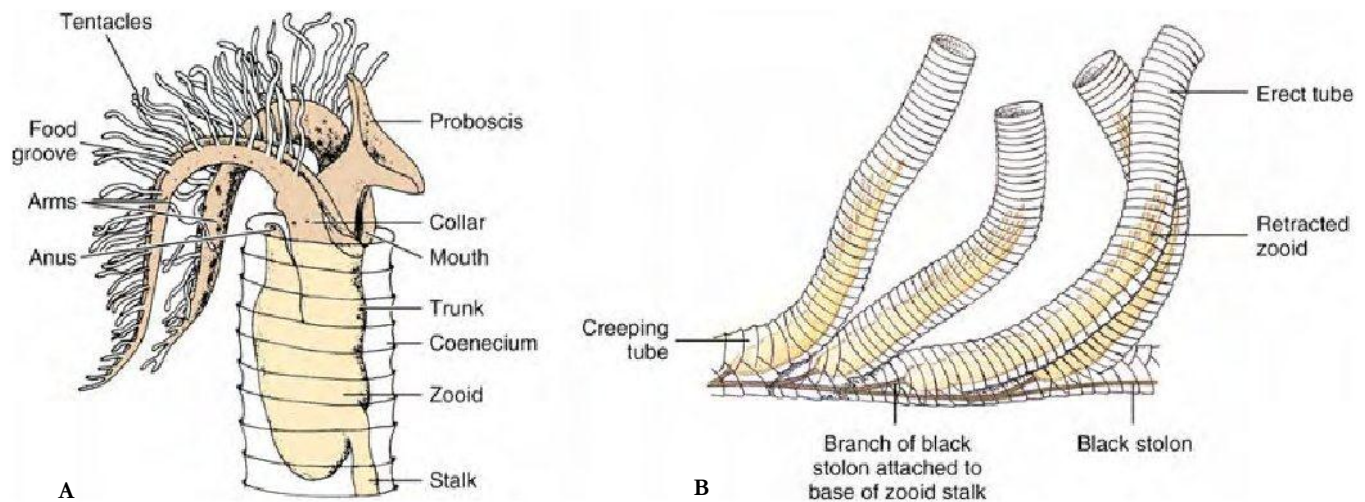
The body of *Cephalodiscus* is divided into the three regions—proboscis, collar, and trunk—characteristic of hemichordates. There is only one pair of gill slits, and the alimentary canal is U-shaped, with the anus near the mouth. The proboscis is shield shaped. At the base of the proboscis are five to nine pairs of branching arms with tentacles containing an extension of the coelomic compartment of the mesosome, as in a lophophore. Ciliated grooves on the tentacles and arms collect food. Some species are dioecious, and others are monoecious. Asexual reproduction by budding may also occur.

In *Rhabdopleura* (Gr. *rhabdos,* rod,   *pleura,* a rib, the side), which is smaller than *Cephalodiscus,* the

Figure 24-5

Cephalodiscus, a pterobranch hemichordate. These tiny (5 to 7 mm) forms live in tubes in which they can move freely. Ciliated tentacles and arms direct currents of food and water toward mouth.

Figure 24-6
A, *Rhabdopleura,* a pterobranch hemichordate in its tube. Individuals live in branching tubes connected by stolons, and protrude the ciliated tentacles for feeding. **B,** Portion of a colony.

members remain together to form a colony of zooids connected by a stolon and enclosed in secreted tubes (Figure 24-6). The collar in these forms bears two branching arms. No gill clefts or glomeruli are present. New individuals are produced by budding from a creeping basal stolon, which branches on a substratum. No pterobranch has a tubular nerve cord in the collar, but otherwise their nervous system is similar to that of Enteropneusta.

The fossil graptolites of the middle Paleozoic era often are placed as an extinct class under Hemichordata. They are important index fossils of the Ordovician and Silurian geological strata. Alignment of graptolites with the hemichordates has been very controversial, but discovery of an organism that seems to be a living graptolite lends strong support to the hypothesis. It has been described as a new species of pterobranch, called *Cephalodiscus graptolitoides.*

Phylogeny and Adaptive Radiation

Phylogeny

Hemichordate phylogeny has long been puzzling. Hemichordates share characters with both echinoderms and chordates. With chordates they share gill slits, which serve primarily for filter feeding and secondarily for breathing, as they do in some protochordates. In addition, a short dorsal, somewhat hollow nerve cord in the collar zone may be homologous to the nerve cord of chordates (Figure 24-7). The buccal diverticulum in the hemichordate mouth cavity, long thought homologous to the notochord of chordates, is now considered a synapomorphy of hemichordates themselves. Early embryogenesis of hemichordates is remarkably like that of echinoderms, and the early tornaria larva is almost identical to the bipinnaria larva of asteroids, suggesting that echinoderms form the sister group of hemichordates and chordates (Figure 24-7). However, Brusca and Brusca* placed lophophorates as the sister group of hemichordates and chordates, required by their proposed synapomorphy for all these groups of a crown of ciliated tentacles containing extensions of the mesocoel. Their hypothesis is not supported by analysis of the base sequence of the gene encoding the small-subunit of rRNA, which indicates a deuterostome

*Brusca, R. C., and G. J. Brusca. 1990. Invertebrates. Sunderland, Massachusetts, Sinauer Associates.
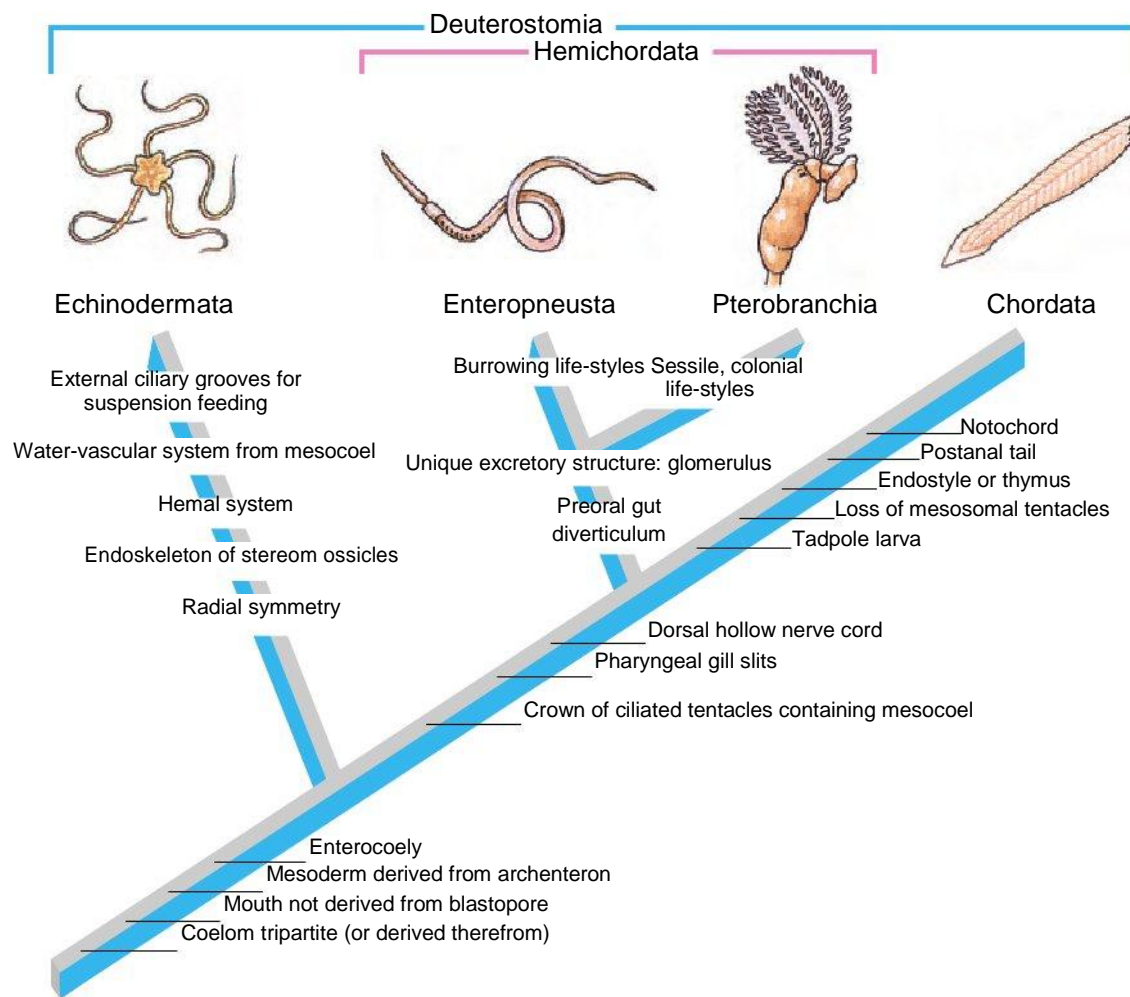
clade (Echinodermata, Hemichordata, and Chordata) and places the lophophorate phyla in superphylum Lophotrochozoa of Protostomia.

Other than their shared deuterostome characters, the relationship of chaetognaths to deuterostome phyla is enigmatic. Sequence analysis of the gene encoding small-subunit rRNA supports placement of chaetognaths among protostomes. Some investigators suggest, however, that chaetognaths are neither protostomes nor deuterostomes but originated independently from an early coelomate lineage.

Adaptive Radiation

Because of their sessile lives and their habitat in secreted tubes in ocean bottoms, where conditions are fairly stable, pterobranchs have undergone little adaptive divergence. They have retained a tentacular type of ciliary feeding. Enteropneusts, on the other hand, although sluggish, are more active than pterobranchs. Having lost their tentaculated arms, they use a proboscis to trap small organisms in mucus, or they eat sand as they burrow and digest organic sediments from the sand. Their evolutionary divergence, although greater than that of pterobranchs, is still modest.

Figure 24-7

Cladogram showing hypothetical relationships among deuterostome phyla. Brusca and Brusca considered the crown of ciliated tentacles (containing extensions of the mesocoel) a character borne by ancestors of lophophorates, hemichordates and chordates. The tentacular crown would have become the lophophore in lophophorate phyla and retained as a primitive character in pterobranchs. Because molecular evidence indicates that lophophorates are protostomes, we removed them from this cladogram; the ciliated tentacular crown in pterobranchs and lophophorates can be considered a convergent character.

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

Summary

Arrowworms (phylum Chaetognatha) are a small group but an important component of marine plankton. They have a well-developed coelom and are effective predators, catching other planktonic organisms with the teeth and chitinous spines around their mouth.

Members of phylum Hemichordata are marine worms that were formerly consid-ered chordates because their buccal diver-ticulum was considered a notochord. How-ever, like chordates, some of them do have gill slits and a hollow, dorsal nerve cord. Divisions of their body (proboscis, collar, trunk) contain the typical deuterostome coelomic compartments (protocoel, meso-coel, metacoel). The hemichordate class Enteropneusta contains burrowing worms that feed on particles strained out of the water by gill slits. Members of class Ptero-branchia are tube dwellers, filter feeding with tentacles. Hemichordates are impor-tant phylogenetically because they show affinities with chordates and echinoderms, and they are the likely sister group of chor-dates.

Review Questions

1. What is evidence that Chaetognatha are deuterostomes? What is evidence that conflicts with this hypothesis?
2. What is the ecological importance of arrowworms?
3. What characteristics do Hemichordata share with Chordata, and how do the two phyla differ?
4. Distinguish Enteropneusta from Pterobranchia.
5. What is the evidence that Hemichordata are related to echinoderms?

Selected References

Barrington, E. J. W. 1965. The biology of Hemichordata and Protochordata. San Francisco, W. H. Freeman & Company. *Concise account of behavior, physiology, and reproduction of hemichordates, urochordates, and cephalochordates.*

Bieri, R., and E. V. Thuesen. 1990. The strange worm *Bathybelos.* Am. Sci. **78:542–549.** Bathybelos *is a peculiar chaetognath with a dorsal nervous system, a characteristic shared in the animal kingdom only with Hemichordata and Chordata. The authors contend that the character in chaetognaths is convergent with that in hemichordates and chordates.*

Svitii, K. A. 1993. It's alive, and it's a graptolite. Discover **14(7):18–19.** *Short account of the discovery of the "living fossil,"* Cephalodiscus graptolitoides.

Thuesen, E. V., and K. Kogure, 1989. Bacterial production of tetrodotoxin in four species of Chaetognatha. Biol. Bull. **176:191–194.** *Chaetognaths use venom to enhance prey capture, and the venom (tetrodotoxin) is produced by bacteria* (Vibrio alginolyticus).

Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

Animal Diversity Web, University of Michigan. Phylum Chordata. General characteristics of chordates, with the following link to urochordates and vertebrates.

Chordata. Arizona's Tree of Life Web Page. An introduction, pictures, characteristics, phylogenetic relationships, and references on chordates.

Introduction to the Hemichordata. University of California at Berkeley Museum of Paleontology site provides photographs and information on the biology and classification of the hemichordates.

Graptolites. Photos and information on these relatives of hemichordates.

OLC Student Center Website

CHAPTER

15

Chordates

General Characteristics, Protochordates, and Ancestry of the Earliest Vertebrates

Two amphioxus in feeding posture.

It's a Long Way From Amphioxus

Along the more southern coasts of North America, half buried in sand on the sea floor, lives a small fishlike translucent animal quietly filtering organic particles from seawater. Inconspicuous, of no commercial value and largely unknown, this creature is nonetheless one of the famous animals of classical zoology. It is amphioxus, an animal that wonderfully exhibits the four distinctive hallmarks of the phylum Chordata—(1) dorsal, tubular nerve cord overlying (2) a supportive notochord, (3) pharyngeal slits for filter feeding, and (4) a postanal tail for propulsion—all wrapped up in one creature with textbook simplicity. Amphioxus is an animal that might have been designed by a zoologist for the classroom. During the nineteenth century, with interest in vertebrate ancestry running high, amphioxus was considered by many to resemble closely the direct ancestor of the vertebrates. Its exalted position was later acknowledged by Philip Pope in a poem sung to the tune of "Tipperary." It ends with the refrain:

It's a long way from amphioxus
   It's a long way to us.
It's a long way from amphioxus
   To the meanest human cuss.
Well, it's good-bye to fins and gill slits
   And its welcome lungs and hair,
It's a long, long way from amphioxus
   But we all came from there.

But amphioxus' place in the sun was not to endure. For one thing, amphioxus lacks one of the most important of vertebrate characteristics, a distinct head with special sense organs and the equipment for shifting to an active predatory mode of life. Absence of a head, together with several specialized features, suggests to zoologists today that amphioxus represents an early departure from the main line of chordate descent. It seems that we are a very long way indeed from amphioxus. Nevertheless, while amphioxus is denied the vertebrate ancestral award, we believe that it more closely resembles the earliest prevertebrate than any other living animal we know. I
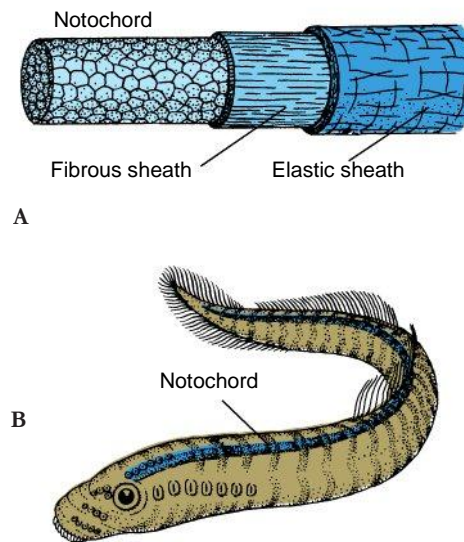
than there is in many other phyla. Ecologically the chordates are among the most adaptable of organic forms and are able to occupy most kinds of habitat. They illustrate perhaps better than any other animal group the basic evolutionary processes of the origin of new structures, adaptive strategies, and adaptive radiation.

Traditional and Cladistic Classification of the Chordates

The traditional Linnaean classification of the chordates (p. 503) provides a simple and convenient way to indicate the taxa included in each major group. However, in cladistic usage, some of the traditional taxa, such as Agnatha and Reptilia, are no longer recognized. Such taxa do not satisfy the requirement of cladistics that only **monophyletic groups are valid** taxonomic entities, that is, groups that contain all known descendants of a single common ancestor. The reptiles, for example, are considered a **paraphyletic** grouping because this group does not contain all of the descendants of their most recent common ancestor (p. 563). The common ancestor of reptiles as traditionally recognized is also the ancestor of birds and mammals. As shown in the cladogram (Figure 25-3), reptiles, birds, and mammals compose a monophyletic clade called Amniota, so named because all develop from an egg having special extraembryonic membranes, one of which is the amnion. Therefore according to cladistics, the reptiles can be grouped only in a negative manner as amniotes that are not birds or mammals; there are no positive or novel features that unite reptiles to the exclusion of birds and mammals. Similarly, agnathans (hagfishes and lampreys) are a paraphyletic grouping because the most recent common ancestor of agnathans is also an ancestor of all remaining vertebrates (the gnathostomes). The reasons why paraphyletic groups are not used in cladistic taxonomy are explained in Chapter 10 (p. 201).

The phylogenetic tree of the chordates (Figure 25-2) and the cladogram of the chordates (Figure 25-3) provide

different kinds of information. The cladogram shows a nested hierarchy of taxa grouped by their sharing of derived characters. These characters may be morphological, physiological, embryological, behavioral, chromosomal, or molecular in nature. Although the cladogram shows the *relative time of* origin of the novel properties of taxonomic groups and their specific positions in the hierarchical system of evolutionary common descent, it contains no timescale or information on ancestral lineages. By contrast, the branches of a phylogenetic tree are intended to represent real lineages that occurred in the evolutionary past. Geological information regarding ages of lineages is added to information from the cladogram to generate a phylogenetic tree for the same taxa.

In our treatment of the chordates, we have retained the traditional Linnaean classification (p. 503) because of its conceptual usefulness and because the alternative—thorough revision following cladistic principles— would require extensive change and virtual abandonment of familiar rankings. However, we have tried to use monophyletic taxa as much as possible, because such usage is consistent with both evolutionary and cladistic taxonomy (see p. 201).

Several traditional divisions of the phylum Chordata used in Linnaean classifications are shown in Table 25-1. A fundamental separation is Protochordata from Vertebrata. Since the former lack a well-developed head, they are also called Acraniata. All vertebrates have a well-developed skull case enclosing the brain and are called Craniata. The vertebrates (craniates) may be variously subdivided into groups based on shared possession of characteristics. Two such subdivisions shown in Table 25-1 are: (1) Agnatha, vertebrates lacking jaws (hagfishes and lampreys), and Gnathostomata, vertebrates having jaws (all other vertebrates) and (2) Amniota, vertebrates whose embryos develop within a fluid-filled sac, the amnion (reptiles, birds, and mammals), and Anamniota, vertebrates lacking this adaptation (fishes and amphib-

ians). The Gnathostomata in turn can be subdivided into Pisces, jawed vertebrates with limbs (if any) in the shape of fins; and Tetrapoda (Gr. *tetras,* four, *podos,* foot), jawed vertebrates with two pairs of limbs. Note that several of these groupings are paraphyletic (Protochordata, Acraniata, Agnatha, Anamniota, Pisces) and consequently are not accepted in cladistic classifications. Accepted monophyletic taxa are shown at the top of the cladogram in Figure 25-3 as a nested hierarchy of increasingly more inclusive groupings.

Four Chordate Hallmarks

The four distinctive characteristics that, taken together, set chordates apart from all other phyla are **notochord, dorsal tubular nerve cord, pharyngeal pouches,** and **postanal tail.** These characteristics are always found at some embryonic stage, although they may be altered or may disappear in later stages of the life cycle.

Notochord

Notochord

The notochord is a flexible, rodlike structure, extending the length of the body. It is the first part of the endoskeleton to appear in the embryo. The notochord is an axis for muscle attachment, and because it can bend without shortening, it permits undulatory movements of the body. In most protochordates and in jawless vertebrates, the notochord persists throughout life (Figure 25-1). In all vertebrates a series of cartilaginous or bony vertebrae are formed from mesenchymal cells derived from blocks of mesodermal cells (somites) lateral to the notochord. In most vertebrates, the notochord is entirely displaced by vertebrae, although remains of the notochord usually persist between or within the vertebrae.

Figure 25-2

Phylogenetic tree of the chordates, suggesting probable origin and relationships. Other schemes have been suggested and are possible. The relative abundance in numbers of species of each group through geological time, as indicated by the fossil record, is suggested by the bulging and thinning of that group's line of descent.

Chordata (animals with notochord at some stage in life cycle)

Euchordata (chordates that retain an axial skeleton throughout life)

Craniata (euchordates with a cranium) = Vertebrata

Gnathostomata (Craniata with jaws)

Teleostomi (bony fishes + tetrapods)

Tetrapoda (four-legged vertebrates)

Amniota (tetrapods with embryos having extraembryonic membranes)

Protochordata

Agnatha

Osteichthyes (bony fishes)

Reptilia

Urochordata (tunicates)

Cephalochordata (lancelets)

Cephalaspidomorphi (lampreys)

Myxini (hagfishes)

Actinopterygii (ray-finned fishes)

Sarcopterygii (lungfishes, lobe-finned fishes)

Amphibia

Chondrichthyes (sharks, rays, chimaeras)

Lepidosauria (lizards, snakes)

Testudines (turtles)

Crocodilia

Aves (birds)

Mammalia (mammals)

Hair, mammary glands

Egg with extraembryonic membranes

Paired limbs used for terrestrial locomotion

Unique supportive elements in skeleton or girdles of fins or legs

Lung or swimbladder derived from gut, bony skeleton

Jaws, 3 pairs semicircular canals, paired appendages, gill filaments lateral to gill support

2 or 3 pairs semicircular canals, mesonephric kidney

Distinct head and brain; specialized sense organs; 1 or more pairs semicircular canals, pronephric kidney, neural crest, neurogenic epidermal placodes

Naked skin, suckerlike oral disc, long larval stage, 7 pairs of gills

Body fusiform, heterocercal caudal fin, placoid scales, cartilaginous skeleton

Naked skin with slime glands, degenerate eyes, notochord persistent

Notochord and nerve cord in free-swimming larvae only

Axial skeleton retained throughout life; muscle somites present

Notochord; dorsal hollow nerve cord; pharyngeal slits; postanal tail

Figure 25-3

Cladogram of living members of phylum Chordata showing probable relationships of monophyletic groups composing the phylum. Each branch in the cladogram represents a monophyletic group. Some derived character states that identify the branchings are shown at right of the branch points. Nesting brackets across the top of the cladogram identify monophyletic groupings within the phylum. The term Craniata, although commonly equated with Vertebrata, is preferred by many authorities because it recognizes that jawless vertebrates (Agnatha) have a cranium but no vertebrae. The lower set of brackets identify the traditional groupings Protochordata, Agnatha, Osteichthyes, and Reptilia. These paraphyletic groups are not recognized in cladistic treatments, but are shown because of widespread use.

TABLE 25.1
Traditional Divisions of the Phylum Chordata

Urochordata (tunicates)	Cephalo-chordata (lancelets)	Myxini (hagfishes)	Cephala-spidomorphi (lampreys)	thyes	Chondrich-thyes (sharks)	Osteichthyes (bony fishes)	Amphibia (amphibians)	Reptilia (reptiles)	Aves (birds)	Mammalia (mammals)

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□||||||||||||||||||||| Χηορδατα ||||||||||||||||||||||||□
□ Προτοχηορδατα |□ (□|||||||||||||||||||| ςερτεβρατα ||||||||||||||||||□
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              (□|||| Αγνατηα |□ (□||||||||||| Γνατηοστοματα ||||||||||||□
                        (□||| Πισχεσ ||□ (□|||||||| Τετραποδα ||||||□
              (□||||||||||| Αναμνιοτα |||||||||||||□ (□||| Αμνιοτα |||||□
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Brain   Dorsal nerve cord

Dorsal Tubular Nerve Cord

In most invertebrate phyla that have a nerve cord, it is ventral to the alimentary canal and is solid, but in chordates the single cord is dorsal to the alimentary canal and is a tube (although the hollow center may be nearly obliterated during growth). The anterior end becomes enlarged to form the brain. The hollow cord is produced in the embryo by the infolding of ectodermal cells on the dorsal side of the body above the notochord. Among the vertebrates, the nerve cord passes through the protective neural arches of the vertebrae, and the anterior brain is surrounded by a bony or cartilaginous cranium.

Pharyngeal slits between aortic arches

Pharyngeal Pouches and Slits

Pharyngeal slits are perforated slitlike openings that lead from the pharyngeal cavity to the outside. They are formed by the inpocketing of the outside ectoderm (pharyngeal grooves)
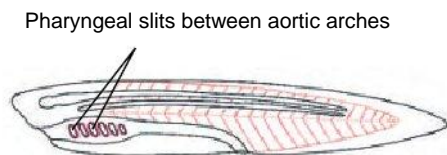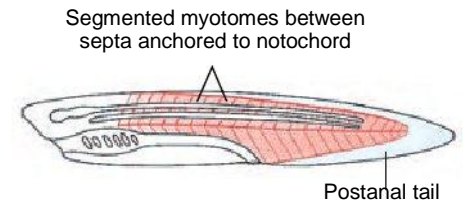
and the evagination, or outpocketing, of the endodermal lining of the pharynx (pharyngeal pouches). In aquatic chordates, the two pockets break through the pharyngeal cavity where they meet to form the pharyngeal slit. In amniotes these pockets may not break through the pharyngeal cavity and only grooves are formed instead of slits. In tetrapod (four-footed) vertebrates the pharyngeal pouches give rise to several different structures, including the Eustachian tube, middle ear cavity, tonsils, and parathyroid glands (see pp. 175–176).

The perforated pharynx evolved as a filter-feeding apparatus and is used as such in the protochordates. Water with suspended food particles is drawn by ciliary action through the mouth and flows out through the pharyngeal slits where food is trapped in mucus. Later, in vertebrates, ciliary action was replaced by a muscular pump that drives water through the pharynx by expanding and contracting the pharyngeal cavity. Also modified were the aortic arches that carry blood through the pharyngeal bars. In protochordates these are simple vessels surrounded by connective tissue. The early fishes added a capillary network having only thin, gas-permeable walls, thus improving efficiency of gas transfer between blood and the water outside. These adaptations led to the evolution of **internal gills,** completing the conversion of the pharynx from a filter-feeding apparatus in protochordates to a respiratory organ in aquatic vertebrates.

Segmented myotomes between septa anchored to notochord

Postanal tail

Postanal Tail

The postanal tail, together with somatic musculature and the stiffening notochord, provides the motility that larval tunicates and amphioxus need for their free-swimming existence. As a structure added to the body behind the end of the digestive tract, it clearly has evolved specifically for propulsion in water. Its efficiency is later increased in fishes with the addition of fins. The tail is evident in humans only as a vestige (the coccyx, a series of small vertebrae at the end of the spinal column) but most other mammals have a waggable tail as adults.

Ancestry and Evolution

Since the mid-nineteenth century when the theory of organic evolution became the focal point for ferreting out relationships among groups of living organisms, zoologists have debated the question of chordate origins. It has been very difficult to reconstruct lines of descent because the earliest protochordates were in all probability soft-bodied creatures that stood little chance of being preserved as fossils

Most of the early efforts to identify kinship of chordates to other phyla are now recognized as based on similarities related to analogy rather than homology. Analogous structures are those that perform similar functions but have altogether different origins (such as wings of birds and butterflies) Homologous structures, on the other hand, share a common origin but may look different (at least superficially) and perform quite different functions. For example, all vertebrate forelimbs are homologous because they are derived from a pentadactyl limb of the same ancestor, even though they may be modified as differently as the human arm and a bird's wing. Homologous structures share a genetic heritage; analogous structures do not. Obviously, only homologous similarities have any bearing in ancestral connections.

even under the most ideal conditions. Consequently, such reconstructions largely come from the study of living organisms, especially from an analysis of early developmental stages, which tend to be more evolutionarily conserved than the differentiated adult forms that they become.

Zoologists at first speculated that chordates evolved within the protostome lineage (annelids and arthropods) but discarded such ideas when they realized that supposed morphological similarities had no developmental basis. Early in this century when further theorizing became rooted in developmental patterns of animals, it became apparent that the chordates must have originated within the deuterostome branch of the animal kingdom. As explained earlier (p. 162 and Figure 8-9), the Deuterostomia, a grouping that includes the echinoderms, hemichordates, lophophorates, and chordates, has several important embryological features that clearly separate it from the Protostomia and establish its monophyly. Thus the deuterostomes are almost certainly a natural grouping of interrelated animals that have their common origin in ancient Precambrian seas. Several lines of anatomical, developmental, and molecular evidence suggest that somewhat later, at the base of the Cambrian

Figure 25-4
Fossil of an early echinoderm, a calcichordate, that lived during the Ordovician period (450 million years BP). It shows affinities with both echinoderms and chordates and may belong to a lineage that was ancestral to chordates.
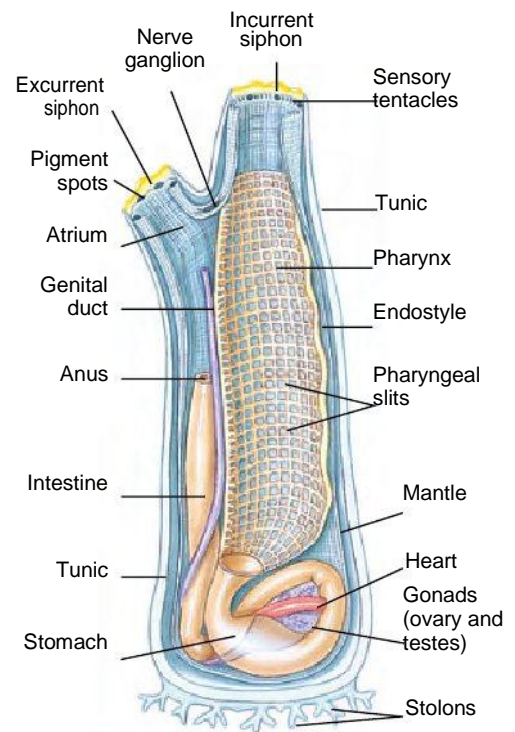
period some 570 million years ago, the first distinctive chordates arose from a lineage related to echinoderms and hemichordates (Figure 25-2; see also Figure 24-7, p. 486).

While modern echinoderms look nothing at all like modern chordates, evolutionary affinity between chordates and echinoderms gains support from fossil evidence. One curious group of fossil echinoderms, the Calcichordata, have pharyngeal slits and possibly other chordate attributes (Figure 25-4, see also p. 475). These small, nonsymmetrical forms have a head resembling a long-toed medieval boot, a series of pharyngeal slits covered with flaps much like the gill openings of sharks, a postanal tail, and structures that are doubtfully interpreted as notochord and muscle blocks. These creatures apparently used their pharyngeal slits for filter feeding, as do protochordates today. Although calcichordates seem to have some of the right chordate characters based on soft anatomy, there is no convincing similarity between the hard skeleton of calcichordates (which was calcium carbonate) and that of vertebrates (which is composed of a complex of calcium

and phosphate). Thus, while we do not yet understand the precise structure of the long-sought chordate ancestor, we do know two living protochordate groups that descended from it. These we will now consider.

Subphylum Urochordata (Tunicata)

The urochordates ("tail-chordates"), more commonly called tunicates, include about 3000 species. They are found in all seas from near shoreline to great depths. Most are sessile as adults, although some are free living. The name "tunicate" is suggested by the usually tough, nonliving **tunic,** or test, that surrounds the animal and contains cellulose (Figure 25-5). As adults, tunicates are highly specialized chordates, for in most species only the larval form, which resembles a microscopic tadpole, bears all the chordate hallmarks. During adult metamorphosis, the notochord (which, in the larva, is restricted

Figure 25-5
Structure of a common tunicate, *Ciona* sp.

to the tail, hence the group name Uro-chordata) and the tail disappear alto-gether, while the dorsal nerve cord becomes reduced to a single ganglion.

Urochordata is divided into three classes: Ascidiacea (Gr. askiolion, lit-tle bag, *acea, suffix*), Larvacea (L. *larva, ghost,* *acea, suffix*), and **Thaliacea (Gr. thalia, luxuriance,** *acea, suffix). Of these the members of* Ascidiacea are by far the most com-mon, diverse, and best known. They are often called "sea squirts" because some species forcefully discharge a jet of water from the excurrent siphon when irritated. All but a few ascidian species are sessile animals, attached to rocks or other hard substrates such as pilings or bottoms of ships. In many areas, they are among the most abun-dant of intertidal animals.

Ascidians may be solitary, colonial, or compound. Each of the solitary and colonial forms has its own test, but among the compound forms many individuals may share the same test (Figure 25-6). In some compound ascidians each member has its own incurrent siphon, but the excurrent opening is common to the group.

Solitary ascidians (Figure 25-5) are usually spherical or cylindrical forms. Lining the tunic is an inner membrane, the **mantle.** On the outside are two projections: the **incurrent siphon,** or oral siphon, which corresponds to the anterior end of the body, and the **excurrent siphon,** or atrial siphon, that marks the dorsal side. When the sea squirt is expanded, water enters the incurrent siphon and passes into a capacious ciliated **pharynx** that is minutely subdivided by gill slits to form an elaborate basketwork. Water passes through the gill slits into an **atrial cavity and out through the** excurrent siphon.

Feeding depends on the forma-tion of a mucous net that is secreted by a glandular groove, the **endostyle,** located along the midventral side of the pharynx. Cilia on gill bars of the pharynx pull the mucus into a sheet that spreads dorsally across the inner face of the pharynx. Food particles brought in the incurrent opening are

Figure 25-6
Compound sea squirt Botryllus sp., common in shallow coastal waters and rock tide pools. Each of the star-shaped patterns represents a colonial arrangement in which the arms of the star are individual organisms, each with its own incurrent siphon at the end of the arm. All are united centrally where they share a common test, forming a compound tunicate.

trapped on the mucous net, which is then worked into a rope and carried posteriorly by cilia into the esophagus and stomach. Nutrients are absorbed in the midgut and indigestible wastes are discharged from the anus, located near the excurrent siphon.

The circulatory system consists of a ventral heart and two large vessels, one on either side of the heart; these vessels connect to a diffuse system of smaller vessels and spaces serving the pharyngeal basket (where respira-tory exchange occurs), the digestive organs, gonads, and other structures. An odd feature found in no other chor-date is that the heart drives the blood first in one direction for a few beats, then pauses, reverses its action, and drives the blood in the opposite direc-tion for a few beats. Another remark-able feature is the presence of strik-ingly high amounts of rare elements in the blood, such as vanadium and nio-bium. The vanadium concentration in the sea squirt *Ciona* may reach 2 mil-lion times its concentration in seawa-ter. The function of these rare metals in the blood is a mystery.

The nervous system is restricted to a **nerve ganglion** and plexus of nerves that lie on the dorsal side of the pharynx. Beneath the nerve ganglion is located the **subneural gland,** con-nected by a duct to the pharynx.
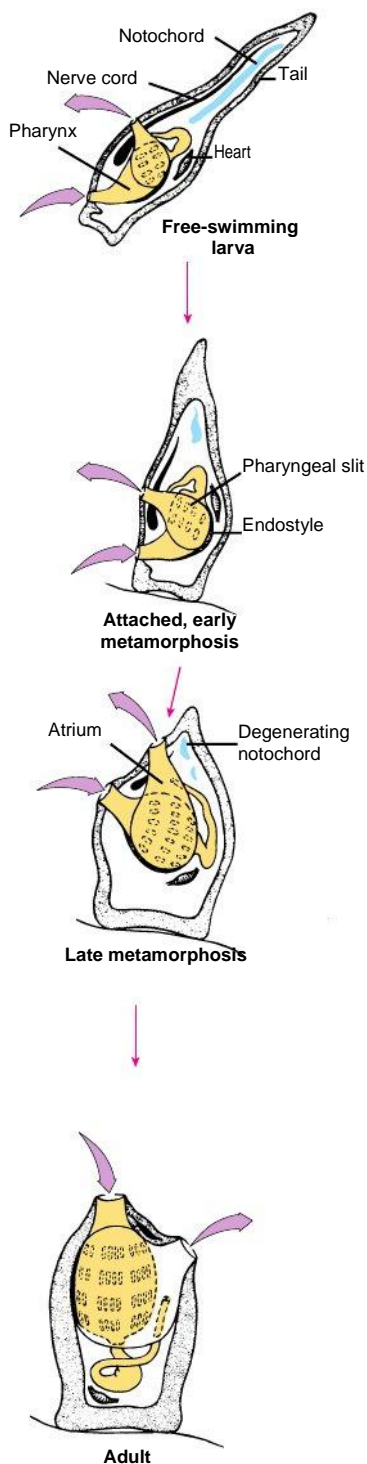
Apparently this gland samples the water coming into the pharynx and may additionally perform an endocrine function concerned with reproduction. A notochord is lacking in adult sea squirts.

Sea squirts are hermaphroditic, with usually a single ovary and a single testis in the same animal. Germ cells are carried by ducts into the atrial cav-ity, and then into the surrounding water where fertilization occurs.

Of the four chief characteristics of chordates, adult sea squirts have only one: pharyngeal slits. However, the lar-val form gives away the secret of their true relationship. The tadpole larva (Figure 25-7) is an elongate, transpar-ent form with all four chordate charac-teristics: notochord, hollow dorsal nerve cord, propulsive postanal tail, and a large pharynx with endostyle and pharyngeal slits. The larva does not feed but swims for some hours before fastening itself vertically by its adhesive papillae to a solid object. It then undergoes a dramatic metamor-phosis (Figure 25-7) to become a ses-sile adult, so modified as to become almost unrecognizable as a chordate.

Tunicates of the class Thaliacea, known as thaliaceans or salps, are barrel- or lemon-shaped pelagic forms with transparent, gelatinous bodies that, despite the considerable size that some species reach, are nearly invisible in sunlit surface waters. They occur singly or in colonial chains that may reach sev-eral meters in length (Figure 25-8). The cylindrical thaliacean body is typically surrounded by bands of circular mus-cle, with incurrent and excurrent siphons at opposite ends. Water pumped through the body by muscular contraction (rather than by cilia as in ascidians) is used for locomotion by a sort of jet propulsion, for respiration, and as a source of particulate food that is filtered on mucous surfaces. Many are provided with luminous organs and give a brilliant light at night. Most of the body is hollow, with the viscera form-ing a compact mass on the ventral side.
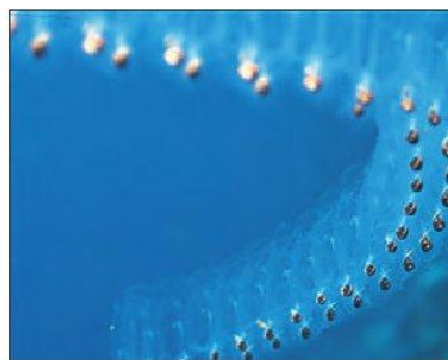
The life histories of thaliaceans are often complex and are adapted to respond to sudden increases in their

Free-swimming larva
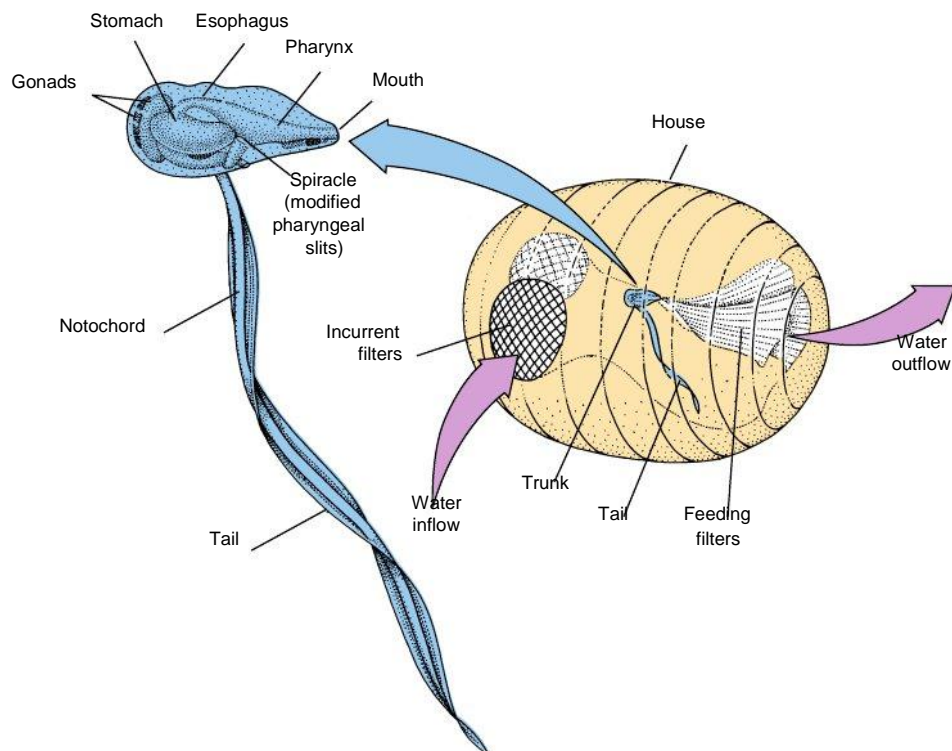
Attached, early metamorphosis

Late metamorphosis

Adult

Figure 25-7
Metamorphosis of a solitary ascidian from a free-swimming tadpole larva stage.

Figure 25-8
Colonial thaliacean. The transparent individuals of this delicate, planktonic species are grouped in a chain. Visible within each individual is an orange gonad, an opaque gut, and a long serrated gill bar.

Figure 25-9
Larvacean adult (left) and as it appears within its transparent house (right), which is about the size of a walnut. When the feeding filters become clogged with food, the tunicate abandons its house and builds a new one.

food supply. The appearance of a phytoplankton bloom, for example, is met by an explosive population increase leading to extremely high density of thaliaceans. Common forms include *Doliolum* and *Salpa,* both of which

reproduce by an alternation of sexual and asexual generations. Thaliaceans are believed to have evolved from sessile ancestors as did the ascidians.

The third tunicate class, the Larvacea (Appendicularia in some classifications) are curious larva-like pelagic creatures shaped like a bent tadpole. In fact their resemblance to the larval stages of other tunicates has given them their class name of Larvacea. They feed by a method unique in the animal world. Each builds a delicate house, a transparent hollow sphere of mucus interlaced with filters and pas-

sages through which the water enters (Figure 25-9). Particulate food trapped on a feeding filter inside the house is drawn into the animal's mouth through a strawlike tube. When the filters become clogged with waste, which happens about every 4 hours, the larvacean abandons its house and builds a new house, a process that takes only a few minutes. Like the thaliaceans, the larvaceans can quickly build up dense populations when food is abundant. At such times scuba diving among the houses, which are about the size of walnuts, is likened to swimming

A

Rostrum · Wheel organ · Dorsal nerve cord · Notochord · Dorsal fin · Myotome · Caudal fin

Oral hood with tentacles · Pharyngeal slits · Pharyngeal bars · Gonad · Hepatic cecum · Atriopore · Intestine · Ventral fin · Anus

Figure 25-10
Amphioxus. This interesting bottom-dwelling cephalochordate illustrates the four distinctive chordate characteristics (notochord, dorsal nerve cord, pharyngeal slits, and postanal tail). The vertebrate ancestor is thought to have had a similar body plan. **A,** Internal structure. **B,** Living amphioxus in typical position for filter feeding. Note the oral hood with tentacles surrounding the mouth.

B

through a snowstorm! Larvaceans are paedomorphic, that is, they are sexually mature animals that have retained the larval body form of their evolutionary ancestors (see the boxed note explaining paedomorphosis on p. 500).

Subphylum Cephalochordata

Cephalochordates are the marine lancelets: slender, laterally compressed, translucent animals about 5 to 7 cm in length (Figure 25-10) that inhabit the sandy bottoms of coastal waters around the world. Lancelets originally bore the generic name *Amphioxus* (Gr. *amphi,* both ends,   oxys, sharp), later surrendered by priority to Branchiostoma (Gr. *branchia,* gills,   *stoma,* mouth). Amphioxus is still used, however, as a convenient common name for all of the approximately 25 species in this diminutive subphylum. Four species of amphioxus are found in North American coastal waters.

Amphioxus is especially interesting because it has the four distinctive

characteristics of chordates in simple form. Water enters the mouth, driven by cilia in the buccal cavity, then passes through numerous pharyngeal slits where food is trapped in mucus, which is then moved by cilia into the intestine. Here the smallest food particles are separated from the mucus and passed into the **hepatic cecum** (liver diverticulum) where they are phagocytized and digested intracellularly. As in tunicates, the filtered water passes first into an **atrium,** then leaves the body by an **atriopore** (equivalent to the excurrent siphon of tunicates).

The closed circulatory system is complex for so simple a chordate. The flow pattern is remarkably similar to that of primitive fishes, although there is no heart. Blood is pumped forward in the **ventral aorta** by peristaltic-like contractions of the vessel wall, then passes upward through branchial arteries (aortic arches) in the pharyngeal bars to paired **dorsal aortas** which join to become a single dorsal aorta. From here the blood is distributed to the body tissues by microcirculation and then is collected in veins, which return

it to the ventral aorta. Lacking both erythrocytes and hemoglobin, their blood is thought to transport nutrients but play little role in gas exchange.

The nervous system is centered around a hollow nerve cord lying above the notochord. Pairs of **spinal nerve roots** emerge at each trunk myomeric (muscle) segment. Sense organs are simple, unpaired bipolar receptors located in various parts of the body. The "brain" is a simple vesicle at the anterior end of the nerve cord.

Sexes are separate. The sex cells are set free in the atrial cavity, then pass out the atriopore to the outside where fertilization occurs. Cleavage is total (holoblastic) and a gastrula is formed by invagination. The larvae hatch soon after deposition and gradually assume the shape of adults.

No other chordate shows the basic diagnostic chordate characteristics as clearly as amphioxus. In addition to the four chordate anatomical hallmarks, amphioxus possesses several structural features that suggest the vertebrate plan. Among these are a hepatic cecum, a diverticulum that
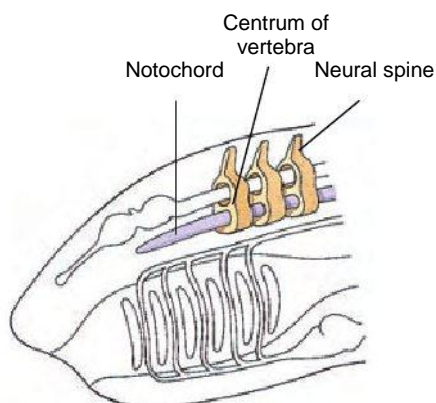
resembles the vertebrate pancreas in secreting digestive enzymes, seg- **mented trunk musculature, and the** basic circulatory plan of more advanced chordates. As discussed later (p. 500), many zoologists consider amphioxus a living descendant of an ancestor that gave rise to both the cephalochordates and the vertebrates. Therefore cephalochordates are, in cladistic terms, the sister group of the vertebrates (Fig-ure 25-3).

Subphylum Vertebrata (Craniata)

The third subphylum of the chordates is the large and diverse Vertebrata. This monophyletic group shares the basic chordate characteristics with the other two subphyla, but in addition it demonstrates a number of novel homologies that the others do not share. The alternative name of the subphylum, Craniata, more accurately describes the group since all have a cranium (bony or cartilaginous braincase) whereas, the jawless fishes lack vertebrae.

Adaptations that Have Guided Vertebrate Evolution

From the earliest fishes to the mammals, the evolution of the vertebrates has been guided by the specialized basic adaptations of living endoskeleton, pharynx and efficient respiration, advanced nervous system, and paired limbs.
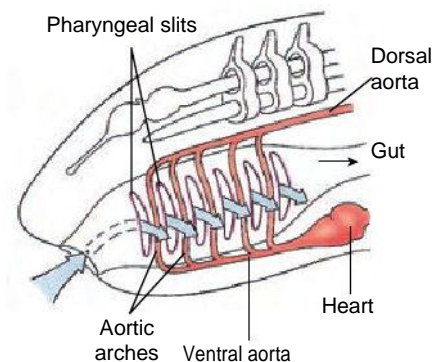

Notochord   Centrum of vertebra   Neural spine

Living Endoskeleton

The endoskeleton of vertebrates, as in the echinoderms, is an internal supportive structure and framework for the body. This internal location is a departure in animal architecture, since invertebrate skeletons generally enfold the body. Exoskeletons and endoskeletons have their own particular sets of advantages and limitations that are related to size (see note on p. 647). For vertebrates, the living endoskeleton possesses an overriding advantage over the dead exoskeleton of arthropods. Growing with the body as it does, the endoskeleton permits almost unlimited body size with much greater economy of building materials. Some vertebrates have become the most massive animals on earth. The endoskeleton forms an excellent jointed scaffolding for muscles and the muscles in turn protect the skeleton and cushion it from potentially damaging impact.

We should note that vertebrates have not wholly lost the protective function of a firm external covering. The skull and thoracic rib cage enclose and protect vulnerable organs. Most vertebrates are further protected with a tough integument, often bearing non-living structures such as scales, hair, or feathers that may provide insulation as well as physical security.

The endoskeleton was probably composed initially of cartilage that later gave way to bone. Cartilage forms a perfectly suitable endoskeleton for aquatic animals. Cartilage is superior to bone for fast growth and is therefore ideal for constructing the first skeletal framework of all vertebrate embryos. In agnathans (hagfish and lampreys), sharks and their kin, and even in some bony fishes such as sturgeons, the adult endoskeleton is composed mostly or entirely of cartilage. Bone appears in the endoskeleton of more derived vertebrates, perhaps because it offers two clear advantages to cartilage. First, it serves as a reservoir for phosphate, an indispensable component of compounds with high-energy bonds, of membranes, and of nucleic acids. Second, only bone could provide the

structural strength required for life on land, where mechanical stresses on the endoskeleton are far greater than they are in water.

Pharyngeal slits   Dorsal aorta   Gut   Heart   Aortic arches   Ventral aorta

Pharynx and Efficient Respiration

The perforated pharynx, present as pharyngeal pouches in all chordates at some stage in their life cycle, evolved for filter-feeding. In primitive chordates (such as amphioxus), water with suspended food particles is drawn through the mouth by ciliary action and flows out through the pharyngeal slits where food is trapped in mucus. As protovertebrates shifted from filter-feeding to a predatory life habit, the pharynx became modified into a muscular feeding apparatus through which water could be pumped by expanding and contracting the pharyngeal cavity. Circulation to the internal gills was improved by addition of capillary beds (lacking in protochordates) and development of a ventral heart and muscular aortic arches. All of these changes supported an increased metabolic rate that would have to accompany the switch to an active life of selective predation.

New Head and Advanced Nervous System

No single system in the body is more strongly associated with functional and structural advancement than is the nervous system. When vertebrate ancestors shifted from filter feeding to active predation, new sensory, motor, and integrative controls became essential for location and capture of larger prey
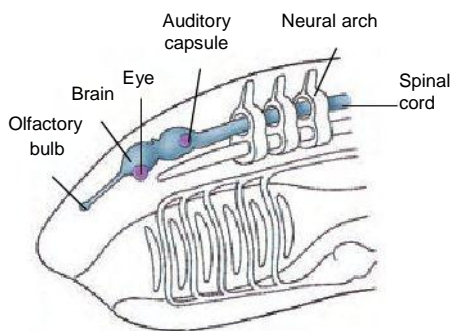
Characteristics of Subphylum Vertebrata

1. Chief diagnostic features of chordates—notochord, dorsal **nerve cord, pharyngeal pouches,** and postanal tail—all present at some stage of the life cycle
2. Integument basically of two divisions, an outer epidermis of stratified epithelium from ectoderm and an inner dermis of connective tissue derived from mesoderm; many modifications of skin among the various classes, such as glands, scales, feathers, claws, horns, and hair
3. Distinctive **endoskeleton** consisting of vertebral column (notochord persistent in jawless fishes which lack vertebrae), limb girdles, and two pairs of jointed appendages derived from somatic mesoderm, and a head skeleton (cranium and pharyngeal skeleton) derived largely from **neural crest cells**
4. Muscular, perforated pharynx; in fishes pharyngeal slits possess gills and muscular aortic arches; in tetrapods the much reduced pharynx is embryonic source of glandular tissue
5. **Many muscles attached to the** skeleton to provide for movement
6. Complete digestive system ventral to the spinal column and provided with large digestive glands, liver, and pancreas
7. Circulatory system consisting of a **ventral heart of two to four chambers;** closed blood vessel system of arteries, veins, and capillaries; blood fluid containing red blood corpuscles with hemoglobin and white corpuscles; paired aortic arches connecting ventral and dorsal aortas and giving off branches to the gills among gill-breathing vertebrates; in terrestrial types modification of the aortic arch plan into pulmonary and systemic systems
8. Well-developed **coelom** largely filled with the visceral systems
9. Excretory system consisting of **paired kidneys** (mesonephric or metanephric types in adults) provided with ducts to drain the waste to cloaca or anal region
10. Highly differentiated brain; 10 or 12 pairs of cranial nerves with both motor and sensory functions usually; a pair of spinal nerves for each primitive myotome; an autonomic nervous system in control of involuntary functions of internal organs; **paired special sense organs** derived from epidermal placodes
11. **Endocrine system of ductless** glands scattered through the body
12. Nearly always separate sexes; each sex containing paired gonads with ducts that discharge their products either into the cloaca or into special openings near the anus
13. **Body plan** consisting typically of **head, trunk,** and **postanal tail; neck** present in some, especially terrestrial forms; two pairs of appendages usually, although entirely absent in some; coelom divided into a pericardial space and a general body cavity; mammals with a thoracic cavity

Brain
Eye
Auditory capsule
Neural arch
Olfactory bulb
Spinal cord

items. Paired special sense organs designed for distance reception evolved. These included paired eyes with lenses and inverted retinas; pressure receptors, such as paired ears designed for equilibrium and later redesigned to include sound reception; electroreceptors that could signal the direction of potential prey; and chemical receptors, including taste receptors and exquisitely sensitive olfactory organs.

Development of the vertebrate head and paired sense organs was largely the result of two embryonic innovations present only in vertebrates: the **neural crest** and **epidermal plac-**

odes. The neural crest, a population of ectodermal cells lying along the length of the embryonic neural tube, contributes to the formation of many different structures, among them the cranium, cranial nerves, branchial skeleton, and the aortic arches. The epidermal placodes are plate-like ectodermal thickenings (the term "placode" derives from a Greek word meaning "plate") that appear anteriorly on either side of the neural tube. These give rise to the nose, eyes, ears, taste receptors, and lateral line mechanoreceptors and electroreceptors. Thus the vertebrate head with its sensory structures located adjacent to the mouth (later equipped with prey-capturing jaws), stemmed from the creation of completely new cell types—a rare event in animal evolution.
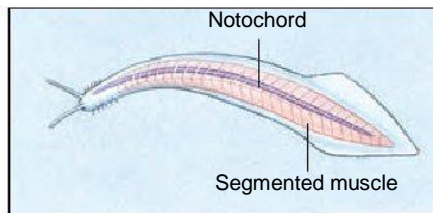
Paired Limbs

Pectoral and pelvic appendages are present in most vertebrates in the form of paired fins or jointed legs. These originated as swimming stabilizers and later became prominently developed into legs for locomotion on land. Jointed limbs are especially suited for life on land because they permit finely graded leveling motions against a substrate.

The Search for the Vertebrate Ancestral Stock

The earliest vertebrate Paleozoic fossils, the jawless ostracoderm fishes we consider at the end of this chapter, share many novel features or organ system development with living vertebrates. These organ systems therefore must have originated in either an early vertebrate or invertebrate chordate lineage. With one exception, hardly any invertebrate chordates are known as fossils. The exception is *Pikaia gracilens,* a ribbon-shaped, somewhat fishlike, creature about 5 cm in length discovered in the famous Burgess Shale of British Columbia (Figure 25-11). *Pikaia* is a mid-Cambrian form that precedes the earliest vertebrate fossils by many millions of years. This fossil possessed
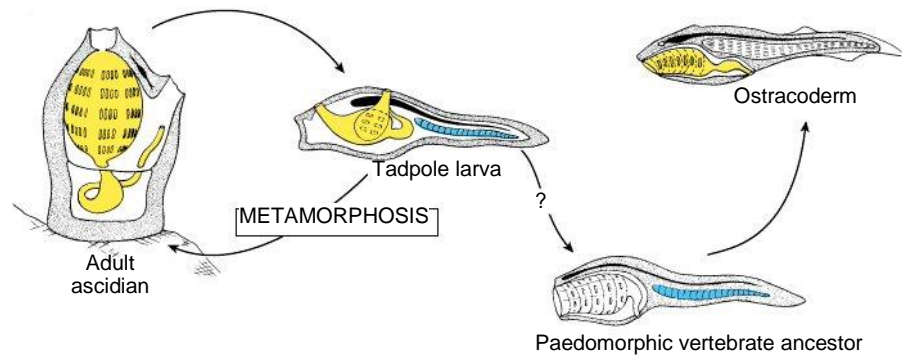
Figure 25-11
Pikaia, the earliest known chordate, from the Burgess Shale of British Columbia, Canada.

Figure 25-12
Garstang's hypothesis of larval evolution. Adult tunicates live on the sea floor but produce a free-swimming tadpole larva. More than 500 million years ago, some larvae began to reproduce in the swimming stage. These evolved into ostracoderms, the first known vertebrates.

both a notochord and characteristic chordate -shaped muscle bands (myotomes). Without question *Pikaia* is a chordate. It shows a remarkable resemblance to living amphioxus, at least in overall body organization, and may in fact be an early cephalochordate. *Pikaia, and a* slightly older similar fossil recently discovered in China, called *Yunnanozoon,* are provocative fossils but, until other Cambrian chordate fossils are discovered their relationship to earliest vertebrates remains uncertain. In the absence of additional fossil evidence, most speculations on vertebrate ancestry have focused on the living cephalochordates and tunicates, since it is widely believed that vertebrates must have emerged from a lineage resembling one of these protochordate groups.

Garstang's Hypothesis of Chordate Larval Evolution

At first glance, tunicates seem unlikely candidates as ancestors for vertebrates. The adult tunicate, which spends it life anchored to some marine surface, lacks a notochord, tubular nerve cord, postanal tail, sense organs, and segmented musculature. Its larva, however, bears all the right qualifications for chordate membership. Called "tadpole" larva because of its superficial resemblance to larval frogs, this tiny, site-seeking form has a notochord, hollow dorsal nerve cord, pharyngeal slits, and postanal tail, as well as a brain and sense organs.

At the time of its discovery in 1869, the tadpole larva was considered a descendant of an ancient free-swimming chordate ancestor of tunicates. The adults then were regarded as degener-

ate, sessile descendants of the free-swimming form. In 1928, Walter Garstang in England introduced fresh thinking into the vertebrate ancestor debate by turning this sequence around; rather than the ancestral tadpole larva giving rise to a degenerative tunicate sessile adult, he suggested that the sessile adults *were* the ancestral stock. The tadpole larva then evolved as an adaptation for spreading to new habitats. Next, Garstang suggested that at some point the tadpole larva failed to metamorphose into an adult, but developed gonads and reproduced in the larval stage. With continued larval evolution, a new group of free-swimming animals appeared (Figure 25-12).

Garstang called this process **paedomorphosis** (Gr. *pais,* child   *morph f,* form), a term describing the evolutionary retention of juvenile or larval traits in the adult body. Garstang departed from previous thinking by suggesting that evolution may occur in larval stages of animals—and in this case, lead to the vertebrate lineage. Paedomorphosis is a well-known phenomenon in several different animal groups (paedomorphosis in amphibians is described on p. 547). Furthermore, Garstang's hypothesis agrees with the embryological evidence. Nevertheless, it remains untested and speculative.

Position of Amphioxus

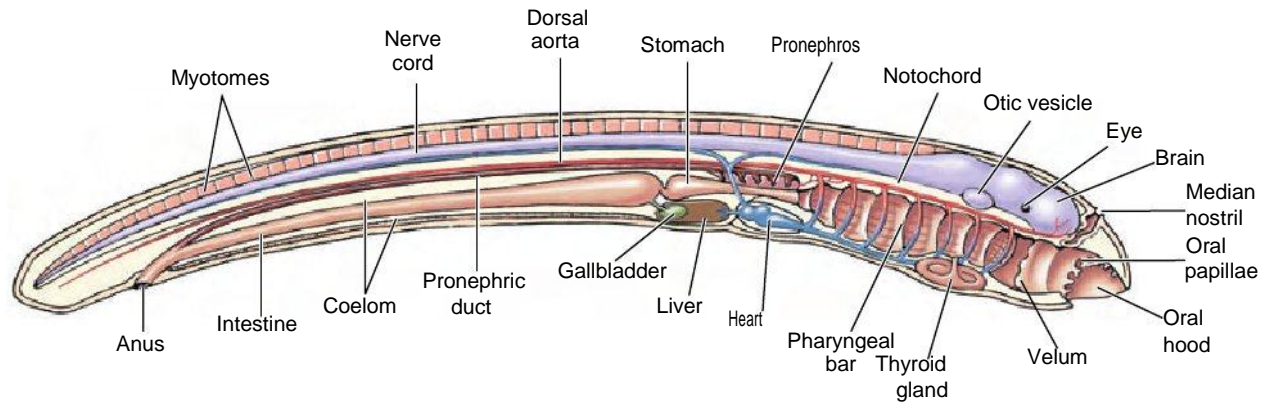For many years zoologists believed that the cephalochordate amphioxus is

the closest living relative of vertebrates. No other protochordate shows the basic diagnostic characteristics of the chordates so well. However, as pointed out in the prologue to this chapter (p. 488), amphioxus is no longer considered a direct ancestor of the vertebrates, although it may closely resemble an ancestor of the vertebrate lineage. It lacks a brain and all of the specialized sensory equipment that characterizes vertebrates. There are no gills in the pharynx and no mouth or pharyngeal musculature for pumping water through the gill slits; movement of water is entirely by the action of cilia.

Paedomorphosis, the displacement of ancestral larval or juvenile features into a descendant adult, can be produced by three different evolutionary-development processes: neoteny, progenesis, and post-displacement. In neoteny, the growth rate of body form is slowed so that the animal does not attain the ancestral adult form at the time it reaches reproductive maturity. Progenesis is the precocious maturation of gonads in a larval (or juvenile) body that then stops growing and never attains the adult body form. In post-displacement, the onset of a developmental process is delayed relative to reproductive maturation, so that the ancestral adult form is not attained at the time of reproductive maturation. Neoteny, progenesis and post-displacement thus describe different ways in which paedomorphosis can happen. Biologists use the inclusive term paedomorphosis to describe the results of these evolutionary-developmental processes.

Figure 25-13

Ammocoete larva, freshwater larval stage of a sea lamprey. Although they resemble amphioxus in many ways, ammocoetes have a well-developed brain, paired eyes, pronephric kidney, and other features lacking in amphioxus but representative of the vertebrate body plan.

Recent studies of the expression of homeobox-containing genes which control the body plan of chordate embryos (homeobox genes are described on p. 169) suggest that the ancestor of both amphioxus and vertebrates was cephalized; it had a head region with a brain and sense organs. In amphioxus and other cephalochordates the notochord grows forward to the anterior tip of the animal, obliterating most traces of the primitive head region. Despite these specializations and others peculiar to modern cephalochordates, many zoologists believe that amphioxus has largely retained the primitive pattern of the immediate prevertebrate condition. Thus cephalochordates are probably the sister group of vertebrates (Figure 25-3).

The Ammocoete Larva of Lampreys as a Model of the Primitive Vertebrate Body Plan

Lampreys (jawless fishes of the class Cephalaspidomorphi, discussed in the next chapter) have a freshwater larval stage known as the ammocoete (Figure 25-13). In body form, appearance, life habit, and most anatomical details, the ammocoete larva resembles amphioxus. In fact, lamprey larvae were given the genus name *Ammocoetes* (Gr. *ammos,* sand, *koit f,* bed, referring to the preferred larval habitat) in the nineteenth century when it was erroneously thought to be an adult cephalochordate, closely allied with amphioxus. Ammo-

coete larvae are so different from adult lampreys that the mistake is understandable; the exact relationship was not explained until metamorphosis into the adult lamprey was observed.

Ammocoete larvae have a long, slender body with an oral hood surrounding the mouth much like amphioxus (Figure 25-13). Ammocoetes are filter feeders, but instead of drawing water by ciliary action into the pharynx as amphioxus does, ammocoetes produce a feeding current by muscular pumping action much like modern fishes. In the floor of the pharynx is an endostyle, as in amphioxus. The endostyle produces a food-ensnaring mucus that is passed directly to the intestine. The arrangement of body muscle into myotomes, the presence of a notochord serving as chief skeletal axis, and the plan of the circulatory system all closely resemble these features in amphioxus.
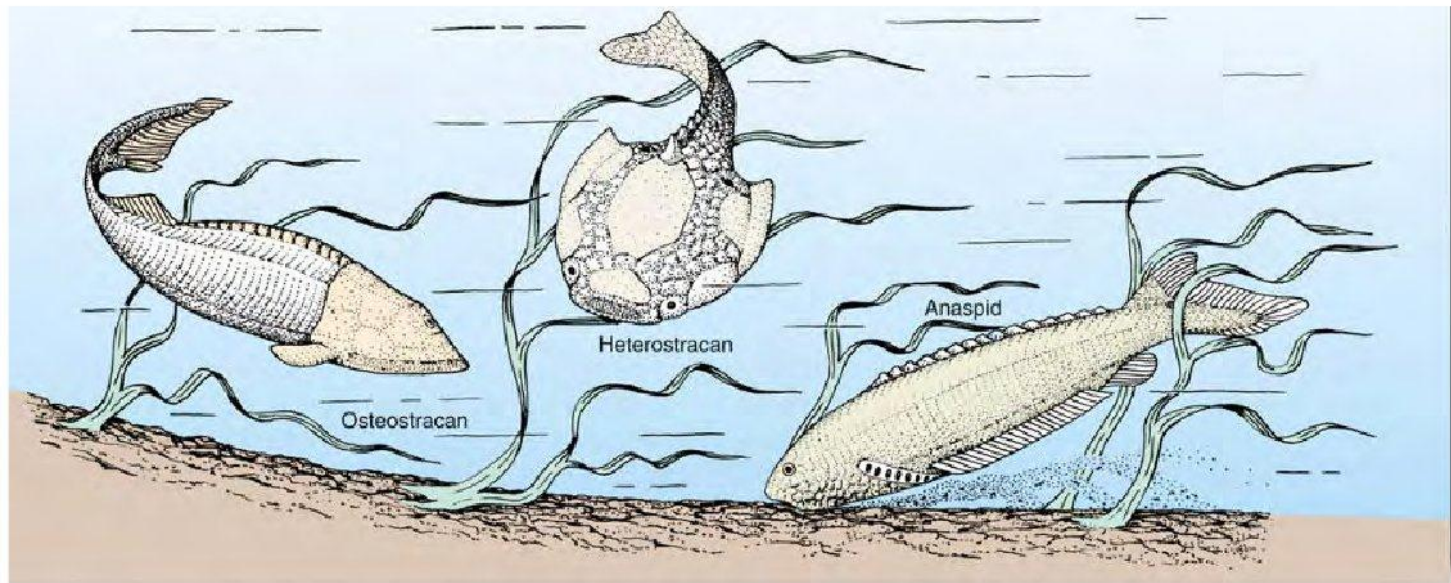
Ammocoetes do have several characteristics lacking in amphioxus that are homologous to those of vertebrates. These include a two-chambered heart (atrium and ventricle), a three-part brain (forebrain, midbrain, hindbrain), special sense organs derived from epidermal placodes (two eyes, one on each side of the midbrain; a median nostril; and auditory vesicles located lateral to the midbrain), a thyroid gland, and a pituitary gland. The kidney is pronephric (p. 670) and conforms to the basic vertebrate plan. Instead of the numerous pharyngeal

slits of amphioxus, there are only seven pairs of pharyngeal pouches and slits in ammocoetes. From pharyngeal bars separating the pharyngeal slits project gill filaments bearing secondary lamellae much like the more extensive gills of modern fishes (see Figure 26-28, p. 527). Ammocoetes also have a true liver replacing the hepatic cecum of amphioxus, a gallbladder, and pancreatic tissue (but no distinct pancreatic gland).

Ammocoete larvae display the most primitive condition for these characteristics of any living vertebrate. It clearly illustrates many shared derived characters of vertebrates that are obscured in the development of other vertebrates. It may approach most closely the supposed body plan of the ancestral vertebrate.

The Earliest Vertebrates: Jawless Ostracoderms

The earliest vertebrate fossils are late Cambrian articulated skeletons from the United States, Bolivia, and Australia. They were small, jawless creatures collectively called ostracoderms (os-trak o-derm) (Gr. *ostrakon,* shell, *derma,* skin), which belong to the Agnatha division of the vertebrates. These earliest ostracoderms lacked paired fins that later fishes found so important for stability (Figure 25-14). The swimming movements of one of the early groups, the **heterostracans** (Gr. *heteros,* different, *ostrakon,*

Figure 25-14
Three ostracoderms, jawless fishes of Silurian and Devonian times. They are shown as they might have appeared while searching for food on the floor of a Devonian sea. All were probably filter-feeders, but employed a strong pharyngeal pump to circulate water rather than the much more limiting mode of ciliary feeding used by their protovertebrate ancestors (presumably resembling amphioxus for this feature). Modern lampreys are believed to be derived from the anaspid group.

shell) (also called pteraspidiforms), must have been clumsy, although sufficient to propel them along the ocean bottom where they searched for food. With fixed circular or slitlike mouth openings they probably filtered small food particles from the water or ocean bottom. However, unlike the ciliary filter-feeding protochordates, ostracoderms sucked water into the pharynx by muscular pumping, an important innovation that suggests to some authorities that ostracoderms may have been mobile predators that fed on soft-bodied animals.

The term "ostracoderm" does not denote a natural evolutionary assemblage but rather is a term of convenience for describing several groups of heavily armored extinct jawless fishes.

During the Devonian period, the heterostracans underwent a major radiation, resulting in the appearance of several peculiar-looking forms varying in shape and length of the snout, dorsal spines, and dermal plates. Without ever evolving paired fins or jaws, these earliest vertebrates flourished for 150 million years until becoming extinct near the end of the Devonian period.

Coexisting with heterostracans throughout much of the Devonian period were **osteostracans** (Gr. *osteon,* bone,   *ostrakon,* shell) (also called cephalaspidiforms). Osteostracans improved the efficiency of their benthic life by evolving paired pectoral fins that provided control over pitch and yaw. This innovation ensured well-directed forward movement. A typical osteostracan, such as *Cephalaspis* (Gr. *kephalf,* head,   *aspis,* shield) (Figure 25-14), was a small animal, seldom exceeding 30 cm in length. It was covered by a well-developed armor—the head by a solid shield and the body by bony plates—but it had no axial skeleton or vertebrae. Their jawless mouth was toothless. Other distinctive features included a sensory lateral line system, paired eyes with complex eye muscle patterns, and inner ears with semicircular canals.

Another group of ostracoderms, the **anaspids,** (Figure 25-14) were more streamlined and more closely resembled modern-day jawless fishes (lamprey, for example) than any other ostracoderm. The evolution of the basic vertebrate head pattern in ostracoderms, although lacking jaws,

was an advance of great significance in vertebrate history. As a group the bottom-feeding ostracoderms enjoyed a respectable radiation in the Silurian and Devonian periods.

The Swedish paleozoologist Erik Stensiö was the first to approach fossil anatomy with the same painstaking attention to minute detail that morphologists have long applied to the anatomical study of living fishes. He developed novel and exacting methods for gradually grinding away a fossil, a few micrometers at a time, to reveal internal features. He was able to reconstruct not only bone anatomy, but nerves, blood vessels, and muscles in numerous groups of Paleozoic and early Mesozoic fishes. His innovative methods are widely used today by paleozoologists.

For decades, geologists have used strange microscopic, toothlike fossils called **conodonts** (Gr. *k|nos,* cone, *odontos,* tooth) to date Paleozoic marine sediments without having any idea what kind of creature originally possessed these elements. The discovery in the early 1980s of fossils of complete conodont animals has changed this situation: conodont elements belonged to a small early marine

vertebrate (Figure 25-15). It is widely believed that as more is learned about conodont animals they will play an important role in understanding the origin of vertebrates. At present, however, their position in vertebrate phylogeny is a matter of debate.

Early Jawed Vertebrates

All jawed vertebrates, whether extinct or living, are collectively called **gnathostomes ("jaw mouth") in con-**trast to the jawless vertebrates, the **agnathans** ("without jaw"). Living agnathans, the naked hagfishes and lampreys, also are often called cyclostomes ("circle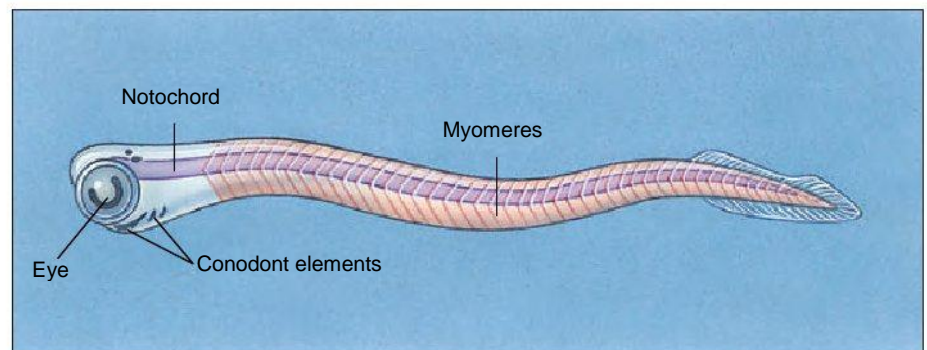 mouth"). The gnathostomes are a monophyletic group since presence of jaws is a derived character state shared by all jawed fishes and tetrapods. Agnathans, however, are defined principally by the absence of a feature—jaws—that characterize the gnathostomes. Therefore the superclass Agnatha may be paraphyletic.

The origin of jaws was one of the most important events in vertebrate evolution. The utility of jaws is obvious: they allow predation on large and active forms of food not available to jawless vertebrates. Ample evidence suggests that jaws arose through modifications of the first two of the serially repeated cartilaginous gill arches. We can see the beginnings of this trend in some ostracoderms where the mouth becomes bordered by strong dermal plates that could be manipulated somewhat like jaws with the gill arch musculature. Later, the anterior gill arches became hinged and bent forward into the characteristic position of vertebrate jaws. Evidence for this remarkable transformation is threefold. First, both gill arches and jaws form from upper and lower bars that bend forward and are hinged in the middle (Figure 25-16). Second, both gill arches and jaws are derived from neural crest cells rather than from mesodermal tissue, the source of most bones. Third, the jaw musculature is homologous to the original gill support musculature. Nearly as remarkable as this drastic morphological remodeling is the subsequent evolutionary fate of jawbone elements—their

Figure 25-15

Restoration of a living conodont animal. Conodonts superficially resembled amphioxus, but they possessed a much greater degree of encephalization (large, paired eyes, possible auditory capsules) and bonelike mineralized elements—all indicating that conodont animals were vertebrates. Conodont elements are believed to be gill-supporting structures or part of a filter-feeding apparatus.

Figure 25-16

How vertebrates got their jaw. The resemblance between jaws and the gill supports of the primitive fishes such as this carboniferous shark suggests that the upper jaw (palatoquadrate) and lower jaw (Meckel's cartilage) evolved from structures that originally functioned as gill supports. The gill supports immediately behind the jaws are hinged like jaws and served to link the jaws to the braincase. Relics of this transformation are seen during the development of modern sharks.

Figure 25-17
Early jawed fishes of the Devonian period, 400 million years ago. Shown are a placoderm (left) and a related acanthodian (right). Jaws and the gill supports from which the jaws evolved develop from neural crest cells, a diagnostic character of vertebrates. Most placoderms were bottom dwellers that fed on detritus although some were active predators. Acanthodians, the earliest-known true jawed fishes, carried less armor than placoderms. Most were marine but several species entered fresh water.

Traditional Linnean Classification of Living Members of Phylum Chordata

Phylum Chordata
  Group Protochordata (Acrania)
    Subphylum Urochordata (u ro-kor-da ta) (Gr. *oura,* tail, L. *chorda,* cord, *ata,* characterized by) **(Tunicata): tunicates.** Notochord and nerve cord in free-swimming larva only; ascidian adults sessile, encased in tunic.
    Subphylum Cephalochordata (sef a-lo-kor-da ta) (Gr. *kephal f,* head, L. *chorda,* cord): **lancelets (amphioxus).** Notochord and nerve cord found along entire length of body and persist throughout life; fishlike in form.
  Group Craniata
    Subphylum Vertebrata (ver te-bra ta) (L. *vertebratus,* backboned). Bony or cartilaginous vertebrae surrounding spinal cord; notochord in embryonic stages, persisting in some fishes; also may be divided into two groups (superclasses) according to presence of jaws.
      Superclass Agnatha (ag na-tha) (Gr. *a,* without, *gnathos,* jaw) **(Cyclostomata): hagfishes, lampreys.** Without true jaws or paired appendages.

(Probably a paraphyletic group.)
      Class Myxini (mik-sin y) (Gr. *myxa,* slime): **hagfishes.** Terminal mouth with four pairs of tentacles; buccal funnel absent; nasal sac with duct to pharynx; 5 to 15 pairs of pharyngeal pouches; partially hermaphroditic.
      Class Cephalaspidomorphi (sef-a-lass pe-do-morf e) (Gr. *kephal f,* head, *aspidos,* shield, *morph f,* form) **(Petromyzones): lampreys.** Suctorial mouth with horny teeth; nasal sac not connected to mouth; seven pairs of pharyngeal pouches.
    Superclass Gnathostomata (na tho-sto ma-ta) (Gr. *gnathos,* jaw, *stoma,* mouth): **jawed fishes, all tetrapods.** With jaws and (usually) paired appendages.
      Class Chondrichthyes (kon-drik thee-eez) (Gr. *chondros,* cartilage, *ichthys,* a fish): **sharks, skates, rays, chimaeras.** Streamlined body with heterocercal tail; cartilaginous skeleton; five to seven gills with separate openings, no operculum, no swim bladder.
      Class Osteichthyes (ost e-ik thee-eez) (Gr. *osteon,* bone,

ichthys, a fish): **bony fishes.** Primitively fusiform body but variously modified; mostly ossified skeleton; single gill opening on each side covered with operculum; usually swim bladder or lung.
      Class Amphibia (am-fib e-a) (Gr. *amphi,* both or double, *bios,* life): **amphibians.** Ectothermic tetrapods; respiration by lungs, gills, or skin; development through larval stage; skin moist, containing mucous glands, and lacking scales.
      Class Reptilia (rep-til e-a) (L. *repere,* to creep): **reptiles.** Ectothermic tetrapods possessing lungs; embryo develops within shelled egg; no larval stage; skin dry, lacking mucous glands, and covered by epidermal scales. (A paraphyletic group.)
      Class Aves (ay veez) (L. pl. of *avis,* bird): **birds.** Endothermic vertebrates with front limbs modified for flight; body covered with feathers; scales on feet.
      Class Mammalia (ma-may lee-a) (L. *mamma,* breast): **mammals.** Endothermic vertebrates possessing mammary glands; body more or less covered with hair; well-developed neocerebrum.

transformation into ear ossicles of the mammalian middle ear (see the note on p. 741).

Among the first jawed vertebrates were the heavily armored placoderms (plak o-derm) (Gr. plax, plate, derma, skin). These first appear in the fossil record in the early Devonian period (Figure 25-17). Placoderms evolved a great variety of forms, some very large (one was 10 m in length!) and grotesque in appearance. They were armored fish covered with diamond-shaped scales or with large plates of bone. All became extinct by the end of the Paleozoic era and appear to have left no descendants. However, the **acanthodians** (Figure 25-17), a group of early jawed fishes that were contemporary with the placoderms, may have given rise to the great radiation of bony fishes that dominate the waters of the world today.

Evolution of Modern Fishes and Tetrapods

Reconstruction of the origins of the vast and varied assemblage of modern living vertebrates is based, as we have seen, largely on fossil evidence. Unfortunately the fossil evidence for the earliest vertebrates is often incomplete and tells us much less than we would like to know about subsequent trends in evolution. Affinities become much easier to establish as the fossil record improves. For instance, the descent of birds and mammals from early tetrapod ancestors has been worked out in a highly convincing manner from the relatively abundant fossil record available. By contrast, the ancestry of modern fishes is shrouded in uncertainty.

Despite the difficulty of clarifying early lines of descent for vertebrates, they are clearly a natural, monophyletic group, distinguished by a large number of shared characteristics. We still do not know, however, from which chordate group the vertebrate lineage originated. Early in their evolution, vertebrates divided into agnathans and gnathostomes. These two groups differ from each other in many fundamental ways, in addition to absence of jaws in the former group and their presence in the latter. The appearance of both jaws and paired fins were major innovations in vertebrate evolution, among the most important reasons for the subsequent major radiations of vertebrates that produced the modern fishes and all of the tetrapods, including you, the reader of this book.

Summary

Phylum Chordata is named for the rodlike notochord that forms a stiffening body axis at some stage in the life cycle of every chordate. All chordates share four distinctive hallmarks that set them apart from all other phyla: notochord, dorsal tubular nerve cord, pharyngeal pouches, and postanal tail. Two of the three chordate subphyla are invertebrates and lack a well-developed head. They are the Urochordata (tunicates), most of which are sessile as adults but all of which have a free-swimming larval stage, and the Cephalochordata (lancelets), fishlike forms that include the famous amphioxus.

The chordates may have descended from echinoderm-like ancestors, probably in the Precambrian period, but the true origin of the chordates is not yet, and may never be, known with certainty. Taken as a whole, chordates have a greater fundamental unity of organ systems and body plan than have many other phyla.

Subphylum Vertebrata includes the backboned members of the animal kingdom (the living jawless vertebrates, the hagfishes and lampreys, actually lack vertebrae but are included with the Vertebrata by tradition because they share numerous homologies with vertebrates). As a group vertebrates are characterized by having a well-developed head, and by their comparatively large size, high degree of motility, and a distinctive body plan that embodies several distinguishing features that permitted the exceptional adaptive radiation of the group. Most important of these are the living endoskeleton that allows continuous growth and provides a sturdy framework for efficient muscle attachment and action, a pharynx perforated with slits (lost or greatly modified in higher vertebrates) with vastly increased respiratory efficiency, advanced nervous system with clear separation of the brain and spinal cord, and paired limbs.

Review Questions

1. What characteristics are shared by the six deuterostome phyla that indicate a monophyletic group of interrelated animals?
2. Explain how the use of a cladistic classification for the vertebrates results in important regroupings of the traditional vertebrate taxa (refer to Figure 25-3). Why are certain traditional groupings such as Reptilia and Agnatha not recognized in cladistic usage?
3. Name four hallmarks shared by all chordates, and explain the function of each.
4. In debating the question of chordate origins, zoologists eventually agreed that the chordates must have evolved within the deuterostome assemblage rather than from a protostome group as earlier argued. What embryological evidences support this view? What

characteristics does the fossil echino-derm group Calcichordata possess that suggest it might closely resemble the ancestor of the chordates?

5. Offer a description of an adult tunicate that would identify it as a chordate, yet distinguish it from any other chordate group.

6. Amphioxus long has been of interest to zoologists searching for a vertebrate ancestor. Explain why amphioxus captured such interest and why it no longer is considered to resemble closely the direct ancestor of the vertebrates.

7. Both sea squirts (urochordates) and lancelets (cephalochordates) are filter-feeding organisms. Describe the filter-feeding apparatus of a sea squirt and explain in what ways its mode of feeding is similar to, and different from, that of amphioxus.

8. Explain why it is necessary to know the life history of a tunicate to understand why tunicates are chordates.

9. List four adaptations that guided vertebrate evolution, and explain how each has contributed to the success of vertebrates.

10. In 1928 Walter Garstang hypothesized that tunicates resemble the ancestral stock of the vertebrates. Explain this hypothesis.

11. Distinguish between ostracoderms and placoderms. What important evolutionary advances did each contribute to vertebrate evolution? What are conodonts?

12. Explain how we think the vertebrate jaw evolved.

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Zoology Links to the Internet

Visit the textbook's web site at www.mhhe.com/zoology to find live Internet links for each of the references below.

Animal Diversity Web, University of Michigan. Phylum Chordata. General characteristics of chordates, with the following links to urochordates and vertebrates.

· Urochordates.
· Vertebrates.——

Phylum Chordata, University of Minnesota.

Introduction to the Urochordata. University of California at Berkeley Museum of Paleontology site provides photographs and information on the biology and classification of the urochordates.

Ascidian News. An online newsletter focusing on the biology of the urochordates. It provides links to other ascidian sites.

Urochordates. Information on all members of this phylum, both sessile and pelagic.

OLC Student Center Website

Fishes

Phylum Chordata
Class Myxini
Class Cephalaspidomorphi
Class Chondrichthyes
Class Actinopterygii
Class Sarcopterygii

Hammerhead shark near the Galápagos Islands.

What Is a Fish?

In common (and especially older) usage, the term fish has often been used to describe a mixed assortment of water-dwelling animals. We speak of jellyfish, cuttlefish, starfish, crayfish, and shellfish, knowing full well that when we use the word "fish" in such combinations, we are not referring to a true fish. In earlier times, even biologists did not make such a distinction. Sixteenth century natural historians classified seals, whales, amphibians, crocodiles, even hippopotamuses, as well as a host of aquatic invertebrates, as fish. Later biologists were more discriminating, eliminating first the invertebrates and then the amphibians, reptiles, and mammals from the narrowing concept of a fish. Today we recognize a fish as an aquatic vertebrate with gills, limbs, if present, in the form of fins, and usually with a skin covered in scales of dermal origin. Even this modern concept of the term "fish" is used for convenience, not as a taxonomic unit, because fishes do not compose a monophyletic group. The common ancestor of the fishes is also an ancestor to the land vertebrates, which we exclude from the term "fish," unless we use the term in an exceedingly nontraditional way. Because fishes live in a habitat that is basically alien to humans, people have rarely appreciated the remarkable diversity of these vertebrates. Nevertheless, whether appreciated by humans or not, the world's fishes have enjoyed an effusive proliferation that has produced an estimated 24,600 living species—more than all other species of vertebrates combined—with adaptations that have fitted them to almost every conceivable aquatic environment. No other animal group threatens their domination of the seas. I

Position in the Animal Kingdom

The fishes are a vast array of distantly related gill-breathing aquatic vertebrates with fins. Fishes are the most ancient and the most diverse of the monophyletic subphylum Vertebrata within the phylum Chordata, constituting five of the nine living vertebrate classes and one-half of the approximately 48,000 recognized vertebrate species. Although they are a heterogeneous assemblage, they exhibit phylogenetic continuity within the group and with the tetrapod vertebrates. The jawless fishes, hagfishes and lampreys, are the living forms that resemble most closely the armored ostracoderms that appeared in the Cambrian period of the Paleozoic. The living jawed fishes, cartilaginous and bony fishes, are related phylogenetically to the acanthodians, a group of jawed fishes that were contemporary with the placoderms of the Silurian and Devonian periods of the Paleozoic. The tetrapod vertebrates, the amphibians, reptiles, birds, and mammals, arose from one lineage of bony fishes, the sarcopterygians (lobe-finned fishes). The evolution of fishes paralled the appearance of numerous advances in vertebrate history.

Biological Contributions

1. The basic vertebrate body plan was established in the common ancestor of all vertebrates. Foremost was the evolution of cellular bone and the **first endoskeleton. The vertebral column** replaced the notochord as the main stiffening axis in most adult vertebrates and provided attachment for the skull, many muscles, and the appendages.
2. With the **brain and spinal cord enclosed** and protected within the cranium and vertebral column, the early fishes were the first animals to house the central nervous system separate from the rest of the body. **Specialized sense organs** for taste, smell, and hearing evolved with a tri-partite brain. Other sensory innovations include an inner ear with semicircular canals, an electrosensory system, intricate lateral line sensory systems, and extrinsic eye muscle.
3. The development of jaws with **teeth** permitted predation of large and active foods. This gave rise to a predator-prey arms race that became a major shaping element in vertebrate evolution through the ages.
4. The evolution of paired pectoral **and pelvic fins supported by shoul-**der and hip girdles provided greatly improved maneuverability and became the precursors of arms and legs of tetrapod vertebrates.
5. Fishes developed the appropriate physiological adaptations that enabled them to invade every conceivable type of aquatic habitat. The origin of lungs and air gulping in early lobe-finned fishes permitted limited penetration of semiterrestrial habitats and prepared for the invasion of land with the evolution of tetrapods.

The life of a fish is bound to its body form. Their mastery of stream, lake, and ocean is revealed in the many ways that fishes have harmonized their life design to the physical properties of their aquatic surroundings. Suspended in a medium that is 800 times more dense than air, a trout or pike can remain motionless, varying its neutral buoyancy by adding or removing air from the swim bladder. Or it may dart forward or at angles, using its fins as brakes and tilting rudders. With excellent organs for salt and water exchange, fishes can steady and finely tune their body fluid composition in their chosen freshwater or seawater environment. Their gills are the most effective respiratory devices in the animal kingdom for extracting oxygen from a medium that contains less than 1/20 as much oxygen as air. Fishes have excellent olfactory and visual senses and a unique lateral line system, which with its exquisite sensitivity to water currents and vibrations pro-vides a "distance touch" in water. Thus in mastering the physical problems of their element, early fishes evolved a basic body plan and set of physiological strategies that both shaped and constrained the evolution of their descendants.

Ancestry and Relationships of Major Groups of Fishes

The fishes are of ancient ancestry, having descended from an unknown free-swimming protochordate ancestor (hypotheses of chordate and vertebrate origins are discussed in Chapter 25). The earliest fishlike vertebrates were a paraphyletic assemblage of jawless **agnathan** fishes, the ostracoderms (Figure 25-14, p. 502). One group of the ostracoderms gave rise to the jawed **gnathostomes** (Figure 26-1).
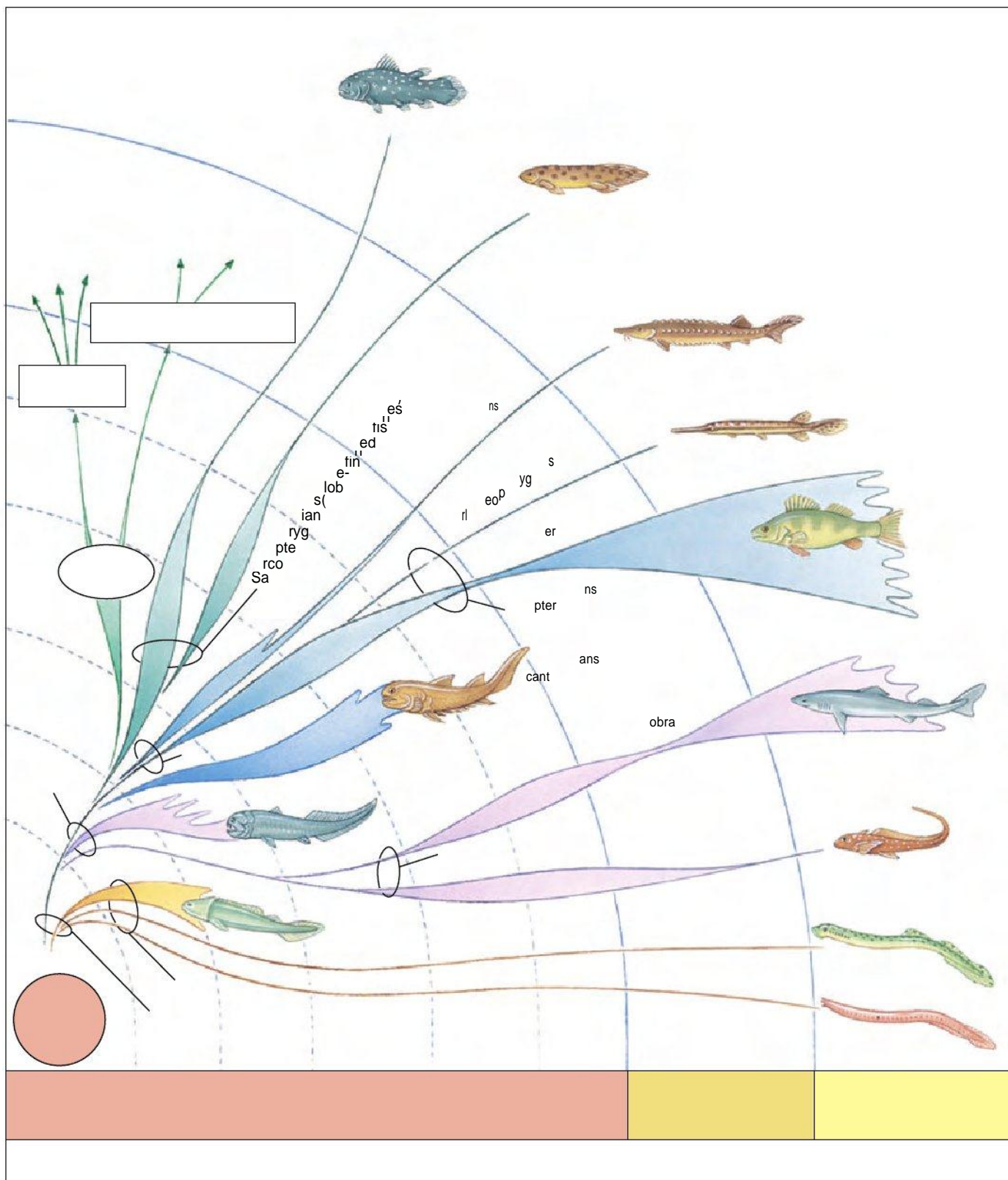
The use of *fishes* as the plural form of *fish* may sound odd to most people accustomed to using *fish* in both the singular and the plural. *Fish* refers to one or more individuals of the some species; *fishes* refers to more than one species.

The jawless agnathans, the least derived of the two groups, include along with the extinct ostracoderms the living **hagfishes** and **lampreys,** fishes adapted as scavengers or parasites. Although hagfishes have no vertebrae and lampreys have only rudimentary vertebrae, they nevertheless are included with the subphylum Vertebrata because they have a cranium and many other vertebrate homologies. The ancestry of hagfishes and lampreys is uncertain; they bear little resemblance to the extinct ostracoderms. Although hagfishes and the more derived lampreys superficially look much alike, they are in fact so different from each other that they have been assigned to separate classes by ichthyologists.
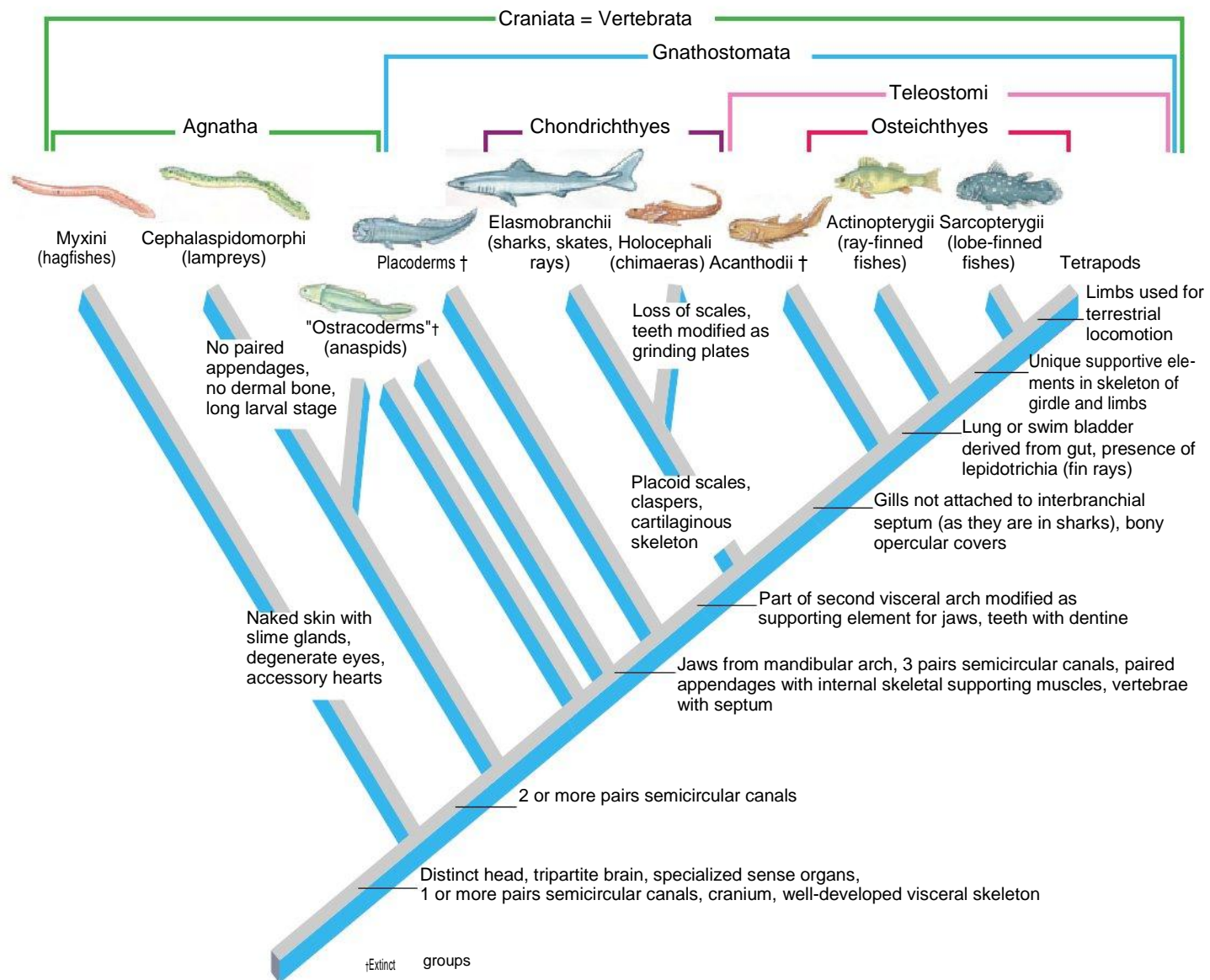
Figure 26-1
Graphic representation of the family tree of fishes, showing the evolution of major groups through geological time. Numerous lineages of extinct fishes are not shown. Widened areas in the lines of descent indicate periods of adaptive radiation and the relative number of species in each group. The fleshy-finned fishes (sarcopterygians), for example, flourished in the Devonian period, but declined and are today represented by only four surviving genera (lungfishes and coelacanth). Homologies shared by the sarcopterygians and tetrapods suggest that they are sister groups. The sharks and rays radiated during the Carboniferous period. They came dangerously close to extinction during the Permian period but staged a recovery in the Mesozoic era and are a secure group today. Johnny-come-latelies in fish evolution are the spectacularly diverse modern fishes, or teleosts, which make up most living fishes.

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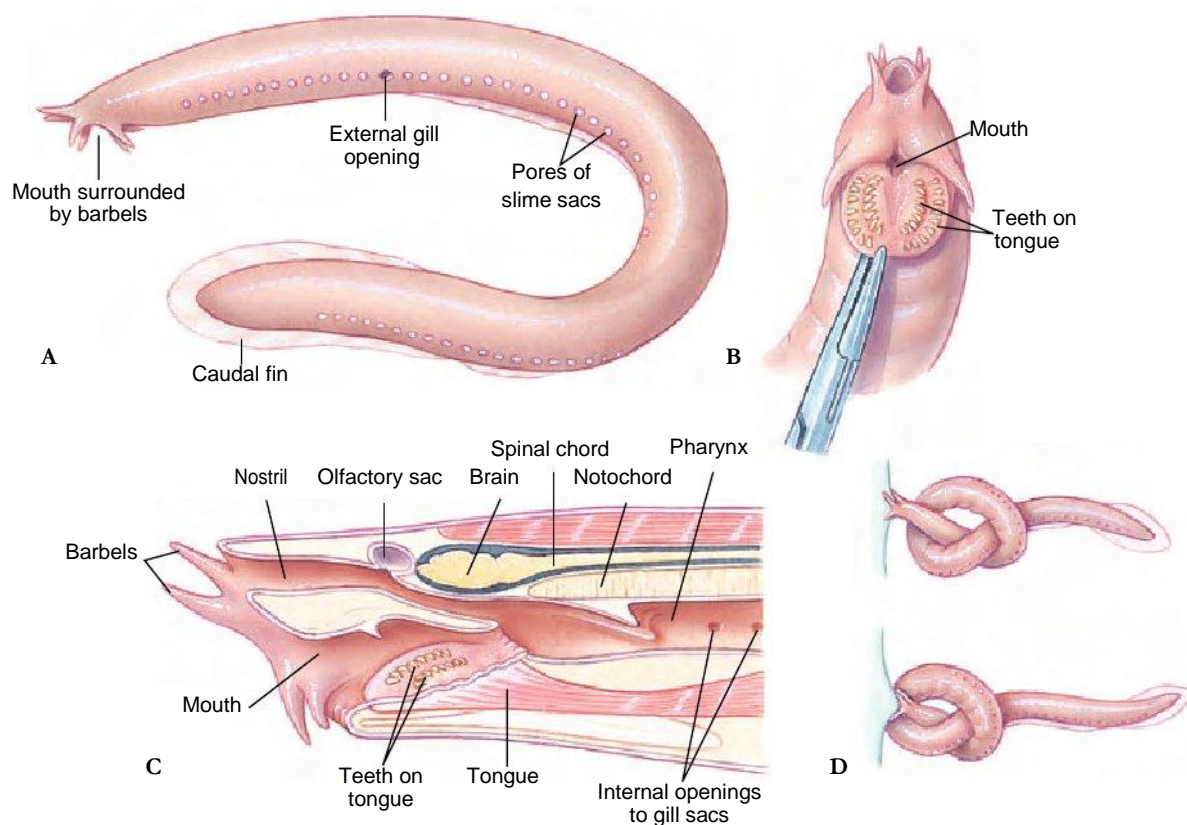v | v | |

Figure 26-2

Cladogram of the fishes, showing the probable relationships of major monophyletic fish taxa. Several alternative relationships have been proposed. Extinct groups are designated by a dagger (†). Some of the shared derived characters that mark the branchings are shown to the right of the branch points. The groups Agnatha and Osteichthyes, although paraphyletic structural grades considered undesirable in cladistic classification, are conveniently recognized in systematics because they share broad structural and functional patterns of organization.

All remaining fishes have paired appendages and jaws and are included, along with the tetrapods (land vertebrates) in the monophyletic lineage of gnathostomes. They appear in the fossil record in the late Silurian period with fully formed jaws, and no forms intermediate between agnathans and gnathostomes are known. By the Devonian period, the Age of Fishes, several distinct groups of jawed fishes were well represented. One of these, the placoderms (p. 505), became ex-tinct in the following Carboniferous period, leaving no direct descendants. A second group, the **cartilaginous fishes** of the class Chondrichthyes (sharks, rays, and chimaeras), lost the heavy dermal armor of early jawed fishes and adopted cartilage rather than bone for the skeleton. Most are active predators with sharklike or ray-like body forms that have undergone only minor changes over the ages. As a group, sharks and their kin flourished during the Devonian and Carbonifer-ous periods of the Paleozoic era but declined dangerously close to extinc-tion at the end of the Paleozoic. They staged a recovery in the early Mesozoic and radiated to form the modest but thoroughly successful assemblage of modern sharks and rays (Figure 26-1).

The other two groups of gnatho-stome fishes, the **acanthodians** (p. 505) and the **bony fishes,** were well represented in the Devonian period. Acanthodians somewhat resem-bled bony fishes but were distinguished

Figure 26-3
The Atlantic hagfish *Myxine glutinosa* (class Myxini). **A,** External anatomy; **B,** Ventral view of head, showing horny plates used to grasp food during feeding; **C,** Sagittal section of head region (note retracted position of rasping tongue and internal openings into a row of gill sacs); **D,** Hagfish knotting, showing how it obtains leverage to tear flesh from prey.

by having heavy spines on all fins except the caudal fin. They became extinct in the lower Permian period. Although the affinities of the acanthodians are much debated, many authors believe that they are the sister group of the bony fishes. The **bony fishes** (Osteichthyes, Figure 26-2) are the domi-nant fishes today. We can recognize two distinct lineages of bony fishes. Of these two, by far the most diverse are the ray-finned fishes (class Actinopterygii), which radiated to form the modern bony fishes. The other lineage, the lobe-finned fishes (class Sarcopterygii), although a relic group today, carry the distinction of being the sister group of the tetrapods. The lobe-finned fishes are represented today by the **lungfishes** and the **coelacanth—** meager remnants of important stocks that flourished in the Devonian period (Figure 26-1). A classification of the major fish taxa is on p. 534.

Superclass Agnatha: Jawless Fishes

Living jawless fishes are represented by approximately 84 species divided between two classes: Myxini (hagfishes) with about 43 species and Cephalaspidomorphi (lampreys) with 41 species (Figures 26-3 and 26-4). Members of both groups lack jaws, internal ossification, scales, and paired fins, and both groups share porelike gill openings and an eel-like body form. In other respects, however, the two groups are morphologically very different. Hagfishes are certainly the least derived of the two, while lampreys bear many derived morphological characters that place them phylogenetically much closer to gnathostomes than to hagfishes. Because of these differences, hagfishes and lampreys have been assigned to separate vertebrate classes, leaving the grouping

"agnatha" as a paraphyletic assemblage of jawless fishes.

Class Myxini: Hagfishes

Hagfishes are an entirely marine group that feeds on annelids, molluscs, crustaceans, and dead or dying fishes. Thus they are not parasitic like lampreys but are scavengers and predators. There are 43 described species of hagfishes, of which the best known in North America are the Atlantic hagfish *Myxine glutinosa* (Gr. *myxa,* slime) (Figure 26-3) and the Pacific hagfish *Eptatretus stouti* (N. L. *ept,* Gr. *hepta,* seven *tretos,* perforated). Although almost completely blind, the hagfish is quickly attracted to food, especially dead or dying fishes, by its keenly developed senses of smell and touch. The hagfish enters a dead or dying animal through an orifice or by digging inside. Using two

Characteristics of Class Myxini

1. Body slender, eel-like, rounded, with naked skin containing **slime glands**
2. **No paired appendages, no dorsal fin** (the caudal fin extends anteriorly along the dorsal surface)
3. **Fibrous and cartilaginous skeleton; notochord persistent**
4. Biting mouth with two rows of eversible teeth
5. Heart with sinus venosus, atrium, and ventricle; **accessory hearts,** aortic arches in gill region
6. Five to 16 pairs of gills with a variable number of gill openings
7. Segmented **mesonephric kidney;** marine, **body fluids isosmotic with seawater**
8. Digestive system **without stomach; no spiral valve or cilia in** intestinal tract
9. Dorsal nerve cord with differentiated brain; **no cerebellum;** 10 pairs of cranial nerves; dorsal and ventral nerve roots united
10. Sense organs of taste, smell, and hearing; **eyes degenerate; one pair semicircular canals**
11. Sexes separate (ovaries and testes in same individual but only one is functional); external fertilization; large yolky eggs, **no larval stage**

Figure 26-4
Sea lamprey, *Petromyzon marinus,* feeding on the body fluids of a dying fish.

toothed, keratinized plates on the tongue that fold together in a pincer-like action, the hagfish rasps away bits of flesh from its prey. For extra leverage, the hagfish often ties a knot in its tail, then passes it forward along the body until it is pressed securely against the side of its prey.

While the unique anatomical and physiological features of the strange hagfishes are of interest to biologists, hagfishes have not endeared themselves to either sports or commercial fishermen. In earlier days of commercial fishing mainly by gill nets and set lines, hagfish often bit into the bodies of captured fish and ate out the contents, leaving behind a useless sack of skin and bones. But as large and efficient otter trawls came into use, hagfishes ceased to be an important pest.

Hagfishes are renowned for their ability to generate enormous quantities of slime. If disturbed or roughly handled, the hagfish exudes a milky fluid from special glands positioned along the body. On contact with seawater, the fluid forms a slime so slippery that the animal is almost impossible to grasp.

Unlike any other vertebrate, the body fluids of hagfishes are in osmotic equilibrium with seawater, as in most marine invertebrates. Hagfishes have several other anatomical and physiological peculiarities, including a low-pressure circulatory system served by three accessory hearts in addition to the main heart positioned behind the gills.

The reproductive biology of hagfishes remains largely a mystery, despite a still unclaimed prize offered more than 100 years ago by the Copenhagen Academy of Science for information on the animal's breeding habits. It is known that females, which in some species outnumber males 100 to one, produce small numbers of surprisingly large, yolky eggs 2 to 7 cm in diameter depending on the species. There is no larval stage.
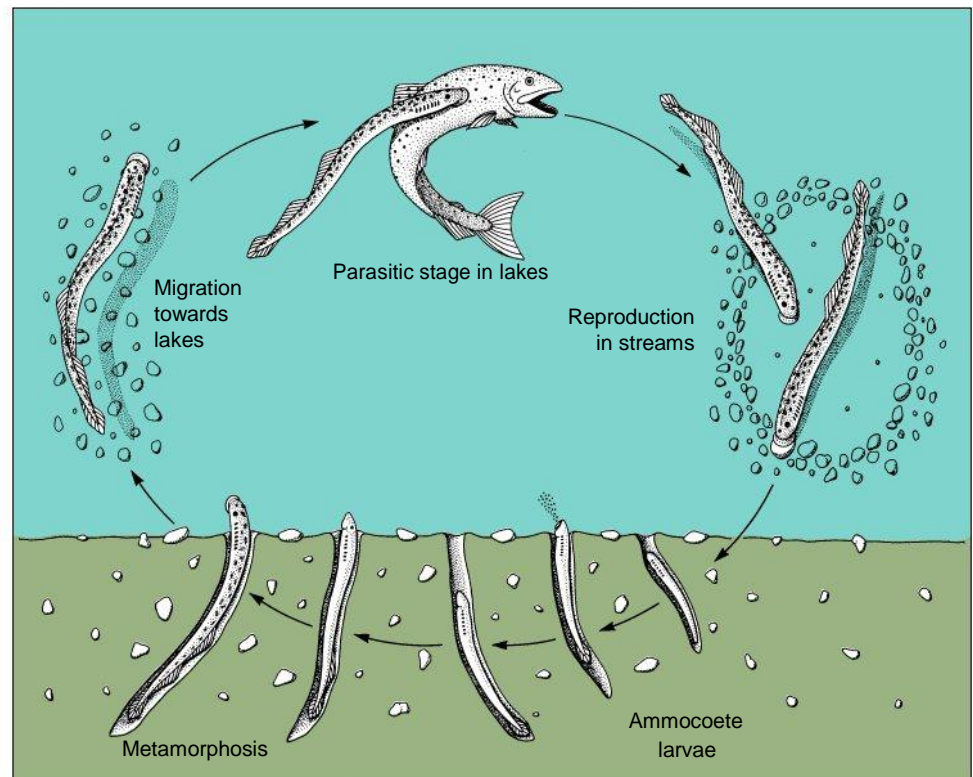
Class Cephalaspidomorphi (Petromyzontes): Lampreys

All the lampreys of the Northern Hemisphere belong to the family Petromyzontidae (Gr. *petros,* stone, *myzon,* sucking). The group name refers to the lamprey's habit of grasping a stone with its mouth to hold position in a current. The destructive marine lamprey *Petromyzon marinus* is found on both sides of the Atlantic Ocean (in America and Europe) and may attain a length of 1 m (Figure 26-4). *Lampetra* (L. *lambo,* to lick or lap up) also has a wide distribution in North America and Eurasia and ranges from 15 to 60 cm long. There are 22 species of lampreys in North America. About half of these belong to the nonparasitic brook type; the others are parasitic. The genus *Ichthyomyzon* (Gr. *ichthyos,* fish, *myzon,* sucking), which includes three parasitic and three nonparasitic species, is restricted to eastern North America. On the west coast of North America the chief marine form is *Lampetra tridentatus.*

Characteristics of Class Cephalaspidomorphi

1. Body slender, eel-like, rounded with naked skin
2. One or two median fins, no **paired appendages**
3. Fibrous and cartilaginous **skeleton; notochord persistent**
4. Suckerlike oral disc and tongue with well-developed keratinized teeth
5. Heart with sinus venosus, atrium, and ventricle; aortic arches in gill region
6. Seven pairs of gills each with external gill opening
7. **Opisthonephric kidney;** anadromous and fresh water; **body fluids osmotically and ionically regulated**
8. Dorsal nerve cord with differentiated brain, small cerebellum **present; 10 pairs cranial nerves;** dorsal and ventral nerve roots separated
9. Digestive system without stomach; intestine with spiral fold
10. Sense organs of taste, smell, hearing; **eyes well developed** in adult; **two pairs semicircular canals**
11. Sexes separate; single gonad without duct; external fertilization; **long larval stage** (ammocoete)

Figure 26-5
Life cycle of the "landlocked" form of the sea lamprey *Petromyzon marinus.*

All lampreys ascend freshwater streams to breed. The marine forms are anadromous (Gr. *anadromos,* running upward); that is, they leave the sea where they spend their adult lives to swim up streams to spawn. In North America all lampreys spawn in winter or spring. Males begin nest building and are joined later by females. Using their oral discs to lift stones and pebbles and vigorous body vibrations to sweep away light debris, they form an oval depression (Figure 26-5). At spawning, with the female attached to a rock to maintain her position over the nest, the male attaches to the dorsal side of her head. As eggs are shed into the nest, they are fertilized by the male. The sticky eggs adhere to pebbles in the nest and quickly become covered with sand. The adults die soon after spawning.

The eggs hatch in about 2 weeks, releasing small larvae (ammocoetes), which are so unlike their parents that early biologists thought they were a separate species. The larva bears a remarkable resemblance to amphioxus and possesses the basic chordate characteristics in such simplified and easily visualized form that it has been considered a chordate archetype (p. 501). After absorbing the remainder of its yolk supply, the young ammocoete, now about 7 mm long, leaves the nest gravel and drifts downstream to burrow in some suitable sandy, low-current area. The larva takes up a suspension-feeding existence while growing slowly for 3 to 7 or more years, then rapidly metamorphoses into an adult. This change involves the eruption of eyes, replacement of the hood by the oral disc with keratinized teeth, enlargement of fins, maturation of gonads, and modification of the gill openings.

Parasitic lampreys either migrate to the sea, if marine, or remain in fresh water, where they attach themselves by their suckerlike mouth to a fish and, with their sharp keratinized teeth, rasp away the flesh and suck out body fluids (Figure 26-6). To promote the flow of blood, the lamprey injects an anticoagulant into the wound. When gorged, the lamprey releases its hold but leaves the fish with a large, gaping wound that is sometimes fatal. The parasitic freshwater adults live 1 to 2 years before spawning and then die; the anadromous forms live 2 to 3 years.
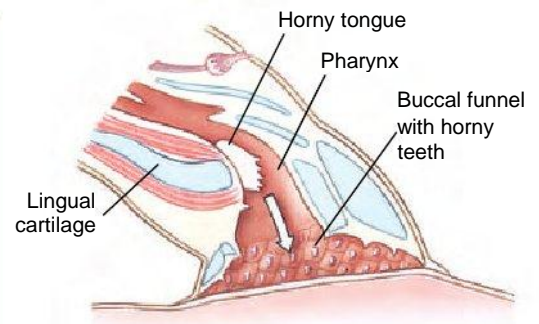
Nonparasitic lampreys do not feed after emerging as adults and their alimentary canal degenerates to a nonfunctional strand of tissue. Within a few months they also spawn and die.

The invasion of the Great Lakes by the landlocked sea lamprey *Petromyzon marinus* in this century has had a devastating effect on the fisheries. No lampreys were present in the Great Lakes west of Niagara Falls until the Welland Ship Canal was built in 1829. Even then nearly 100 years elapsed
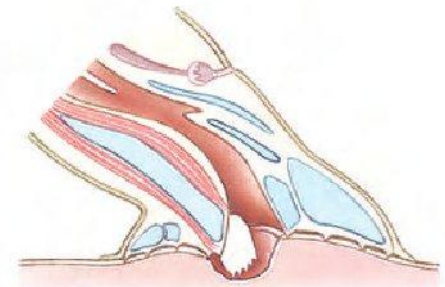
Characteristics of Class Chondrichthyes

1. Large (average about 2 m), body **fusiform, or dorsoventrally depressed**, with a heterocercal caudal fin (diphycercal in chimaeras) (Figure 26-16); paired pectoral and pelvic fins, two dorsal median fins; pelvic fins in male modified for "claspers"
2. **Mouth ventral; two olfactory sacs** that do not open into the mouth cavity in elasmobranchs; nostrils open into mouth cavity in chimaeras; jaws modified from pharyngeal arch
3. Skin with **placoid scales** or naked in elasmobranchs (Figure 26-18); skin naked in chimaeras; teeth of modified placoid scales and serially replaced in elasmobranchs; teeth modified as grinding plates in chimaeras
4. **Endoskeleton entirely cartilaginous; notochord persistent but** reduced; vertebrae complete and separate in elasmobranchs; vertebrae present but centra absent in chimaeras; appendicular, girdle, and visceral skeletons present; cranium sutureless
5. Digestive system with J-shaped stomach (stomach absent in chimaeras); **intestine with spiral valve;** often with large oil-filled liver for buoyancy
6. Circulatory system of several pairs of aortic arches; dorsal and ventral aorta, capillary and venous systems, hepatic portal and renal portal systems; four-chambered heart with sinus venosus, atrium, ventricle, and conus arteriosus
7. Respiration by means of five to seven pairs of gills leading to exposed gill slits in elasmobranchs; four pairs of gills covered by an operculum in chimaeras
8. No swim bladder or lung
9. Opisthonephric kidney and rectal gland; blood isosmotic or slightly hyperosmotic to sea water; **high concentrations of urea and trimethylamine oxide in blood**
10. Brain of two olfactory lobes, two cerebral hemispheres, two optic lobes, cerebellum, medulla oblongata; 10 pairs of cranial nerves; three **pairs of semicircular canals**
11. Senses of smell, vibration reception (lateral line system), vision, and electroreception well developed; inner ear opens to outside via endolymphatic duct
12. Sexes separate; gonads paired; reproductive ducts open into cloaca (separate urogenital and anal openings in chimaeras); oviparous, ovoviviparous, or viviparous; direct development; **fertilization internal**

Attachment to fish with horny teeth and suction

Tongue protruded for rasping flesh

Figure 26-6
How the lamprey uses its horny tongue to feed. After firmly attaching to a fish by its sucker, the protrusible tongue rapidly rasps an opening through the fish's integument. Body fluid, abraded skin, and muscle are eaten.
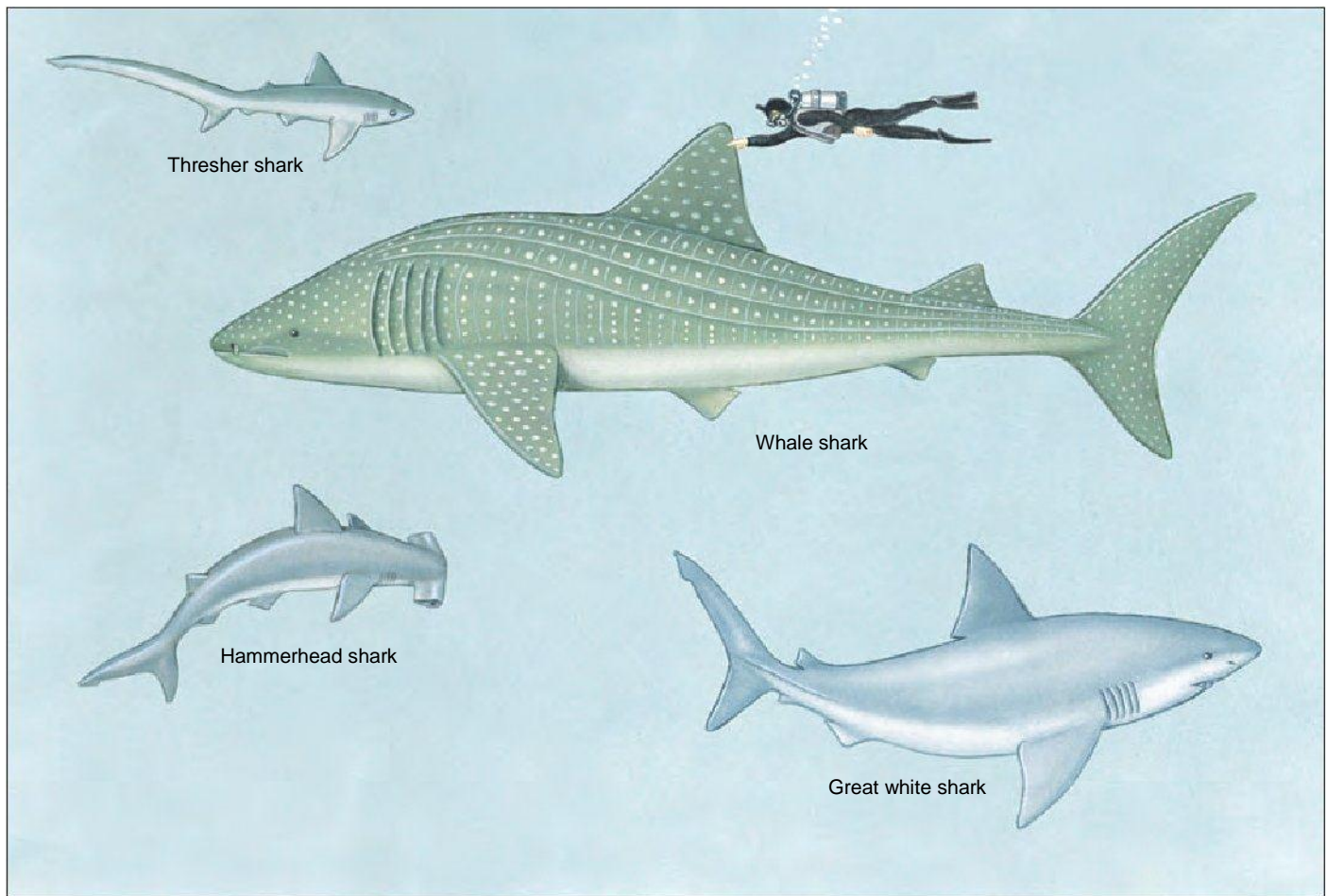
before sea lampreys were first seen in Lake Erie. After that the sea lamprey spread rapidly and was causing extraordinary damage in all the Great Lakes by the middle 1940s. No fish species was immune from attack, but the lampreys preferred lake trout, and this multimillion dollar fishing industry was brought to total collapse in the late 1950s. Lampreys then turned to rainbow trout, whitefish, burbot, yellow perch, and lake herring, all important commercial species. These stocks were decimated in turn. The lampreys then began attacking chubs and suckers. Coincident with decline in attacked species, sea lampreys themselves

began to decline after reaching a peak abundance in 1951 in Lakes Huron and Michigan and in 1961 in Lake Superior. The fall has been attributed both to depletion of food and to the effectiveness of control measures (mainly chemical larvicides in selected spawning streams). Lake trout, aided by a restocking program, are now recovering. Wounding rates are low in Lake Michigan but still high in some lakes. Fishery organizations are now experimenting with the release of sterilized male lampreys into spawning streams; when fertile females mate with sterilized males the female's eggs fail to develop.

Class Chondrichthyes: Cartilaginous Fishes

There are nearly 850 living species in the class Chondrichthyes, an ancient, compact, and highly developed group. Although a much smaller and less diverse assemblage than the bony fishes, their impressive combination of well-developed sense organs, powerful jaws and swimming musculature, and predaceous habits ensures them a secure and lasting place in the aquatic community. One of their distinctive features is their cartilaginous skeleton.

Figure 26-7

Diversity in sharks of the subclass Elasmobranchii. The thresher shark *Alopias vulpinus,* exceptional because of its long upper tail lobe, may exceed 4 m in length. The great white shark *Carcharodon carcharias,* largest and most notorious of dangerous sharks, is a heavy-bodied, spindle-shaped shark that may reach 6 m in length. The nine species of hammerheads (genus *Sphyrna)* are distinguished from all other sharks by the flattened head with hammerlike lobes bearing eyes and nostrils on the ends. The whale shark *Rhincodon typus* is the world's largest fish, reaching 12 m in length. It is a suspension feeder that feeds on plankton collected on a sievelike mesh over its gills.

Although calcification may be extensive in their skeletons, bone is entirely absent throughout the class—a curious evolutionary feature, since the Chondrichthyes are derived from ancestors having well-developed bone. Almost all chondrichthyans are marine; only 28 species live primarily in fresh water.

With the exception of whales, sharks include the largest living vertebrates. The larger sharks may reach 12 m in length. Dogfish sharks so widely studied in zoological laboratories rarely exceed 1 m.

Subclass Elasmobranchii: Sharks, Skates, and Rays

There are nine living orders of elasmobranchs, numbering about 815 species.

Coastal waters are dominated by the requiem sharks, order Carcharhiniformes, which consist of typical-looking sharks such as the tiger and bull sharks and more bizarre forms, including the hammerheads (Figure 26-7). The order Lamniformes contains several large, pelagic sharks dangerous to humans, including the great white and mako sharks. Dogfish sharks, familiar to generations of comparative anatomy students, are in the order Squaliformes. Skates and several groups of rays (sawfish rays, electric rays, stingrays, eagle rays, manta rays, and devil rays) belong to the order Rajiformes.

Much has been written about the propensities of sharks to attack humans, both by those exaggerating their ferocious nature and by those seeking to

write them off as harmless. It is true, as the latter group of writers argues, that sharks are by nature timid and cautious. But it also is a fact that certain of them are dangerous to humans. There are numerous authenticated cases of shark attacks by *Carcharodon* (Gr. *karcharos,* sharp, *odous,* tooth), the great white shark (reaching 6 m); mako sharks *Isurus* (Gr. *is,* equal, *ouros,* tail); the tiger shark *Galeocerdo* (Gr. *galeos,* shark, *kerd|,* fox); and hammerhead sharks *Sphyrna* (Gr. *sphyra,* hammer). More shark casualties have been reported from the tropical and temperate waters of the Australian region than from any other. During World War II there were several reports of mass shark attacks on the victims of ship sinkings in tropical waters.