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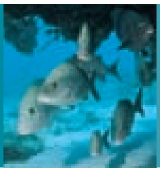


chapter sixteen

Fishes

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 a gill-breathing, ectothermic, aquatic vertebrate that possesses fins, and skin that is usually covered with scales. Even this modern concept of the term "fish" is controversial, at least as a taxonomic unit, because fishes do not compose a monophyletic group. The common ancestor of fishes is also an ancestor to land vertebrates, which we exclude from the term "fish," unless we use the term in an exceedingly non-traditional 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.

Grey snappers (*Lutjanus griseus*) in the Florida Keys.

The life of a fish is bound to its body form. Mastery of river, lake, and ocean is revealed in the many ways that fishes have harmonized their 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 its 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, bony 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 provides 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.

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. Both plural forms are correct but zoologists use* fishes *to mean more than one kind of fish.*

Ancestry and Relationships of Major Groups of Fishes

Fishes are of ancient ancestry, having descended from an unknown free-swimming protochordate ancestor (hypotheses of chordate and vertebrate origins are discussed in Chapter 15). The earliest fishlike vertebrates were a paraphyletic assemblage of jawless **agnathan** fishes, the ostracoderms (see figure 15.10, p. 297). One group of ostracoderms gave rise to the jawed **gnathostomes** (see figure 15.13).

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 within 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.

All remaining fishes have paired appendages and jaws and are included, along with 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 (see figure 15.13, p. 298), became extinct in the following Carboniferous period, leaving no descendants. A second group, the **cartilaginous fishes** of class Chondrichthyes (sharks, rays, and chimaeras), lost the heavy dermal armor of the early jawed fishes and adopted cartilage rather than bone for the skeleton. Most are active predators with a sharklike body form that has undergone only minor changes over the ages.

Of all gnathostomes, **bony fishes** (the Osteichthyes) radiated most extensively and are the dominant fishes today (figure 16.1). 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 modern bony fishes. The other lineage, **lobe-finned fishes** (class Sarcopterygii), although a relic group today, carry the distinction of being the sister group of tetrapods. The lobe-finned fishes are represented today by **lungfishes** and the **coelacanth**—meager remnants of important stocks that flourished in the Devonian period (figure 16.1). A classification of major fish taxa is on p. 322.

Superclass Agnatha: Jawless Fishes

Living jawless fishes are represented by approximately 84 species almost equally divided between two classes: Myxini (hagfishes) and Cephalaspidomorphi (lampreys) (figure 16.2). 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. Lampreys bear many derived morphological characters that place them phylogenetically much closer to jawed bony fishes 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.

Hagfishes: Class Myxini

Hagfishes are an entirely marine group that feeds on dead or dying fishes, annelids, molluscs, and crustaceans. 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 16.3) and the Pacific hagfish *Eptatretus stouti* (NL, *ept*<Gr. *hepta,* seven, + *tretos,* perforated). Although almost completely blind, hagfishes are quickly attracted to food, especially dead or dying fish, by their keenly developed senses of smell and touch. After attaching itself to its prey by means of toothed plates, a hagfish thrusts its tongue forward to rasp off pieces of tissue. For extra leverage, a hagfish often ties a knot in its tail, then passes the knot forward along its body until it is pressed securely against the side of its prey (figure 16.3).

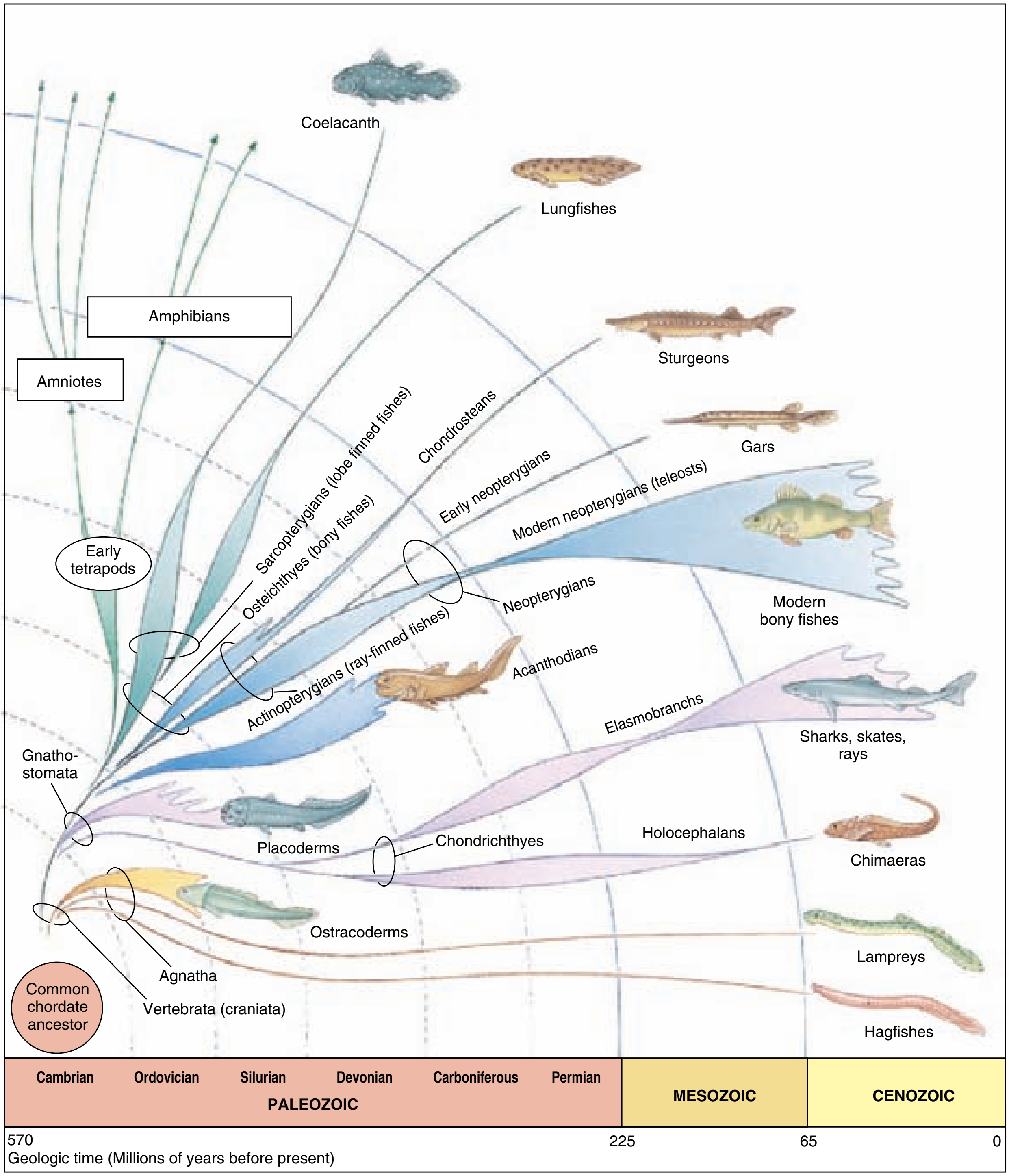


figure 16.1

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 lobe-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 include most living fishes. Note that the class Osteichthyes is a paraphyletic group because it does not include their descendants, the tetrapods; in cladistic usage the Osteichthyes includes the tetrapods (see figure 16.2).

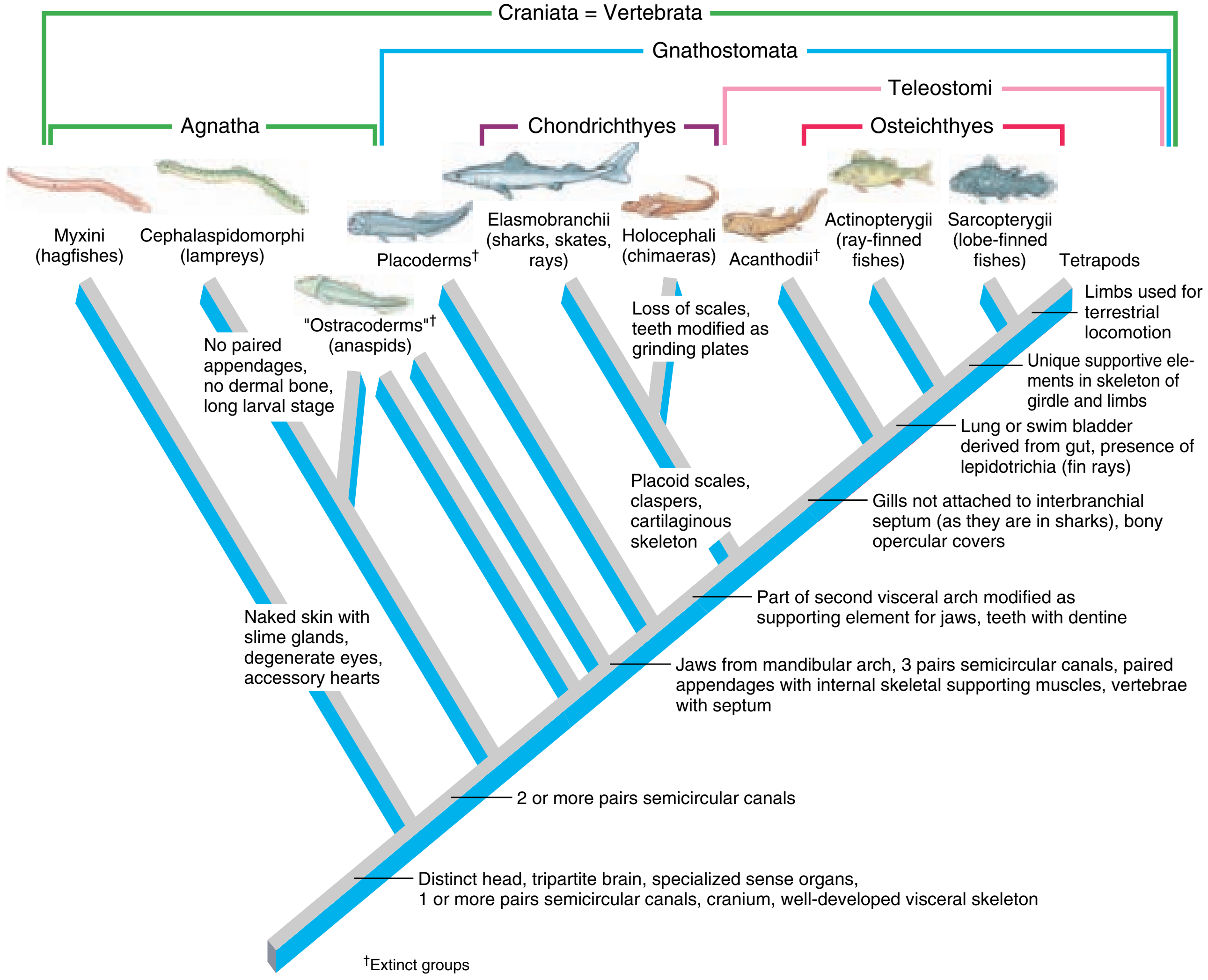


figure 16.2

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.

Unlike any other vertebrate, 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. Hagfishes are also renowned for their ability to generate enormous quantities of slime.

The reproductive biology of hagfishes remains largely a mystery. Both male and female gonads are found in each animal, but only one gonad becomes functional. Females produce small numbers of surprisingly large, yolky eggs 2 to 7 cm in diameter, depending on the species. There is no larval stage and growth is direct.

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.

characteristics of jawless fishes

1. Slender, **eel-like** body
2. Median fins but **no** paired appendages
3. **Fibrous** and **cartilaginous skeleton;** notochord persistent; no vertebrae
4. Biting mouth with two rows of eversible teeth in hagfishes; suckerlike oral disc with well-developed teeth in lampreys
5. Heart with one atrium and one ventricle; hagfishes with three accessory hearts; aortic arches in gill region
6. Five to 16 pairs of gills and a single pair of gill apertures in hagfishes; 7 pairs of gills in lampreys
7. **Pronephric kidney** anteriorly and **mesonephric kidney** posteriorly in hagfishes; mesonephric kidney only in lampreys
8. Dorsal nerve cord with differentiated brain; 8 to 10 pairs of cranial nerves
9. Digestive system **without stomach;** intestine with spiral valve and cilia in lampreys; both lacking in intestine of hagfishes
10. Sense organs of taste, smell, hearing; eyes poorly developed in hagfishes but moderately well developed in lampreys; one pair of **semicircular canals** (hagfishes) or two pairs (lampreys)
11. External fertilization; both ovaries and testes present in an individual but gonads of only one sex functional and no larval stage in hagfishes; separate sexes and long larval stage with radical metamorphosis in lampreys

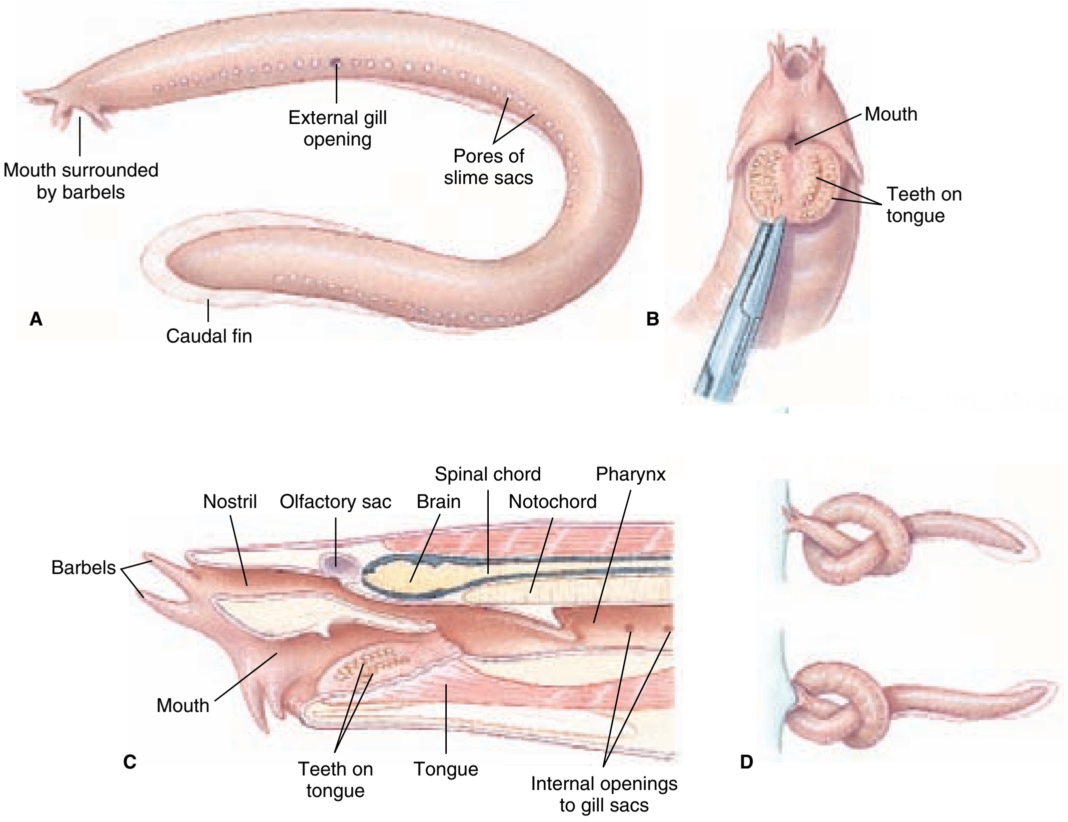


figure 16.3

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.

figure 16.4
Sea lamprey, *Petromyzon marinus,* feeding on the body fluids of a dying fish.

Lampreys: Class Cephalaspidomorphi

Of the 41 described species of lampreys distributed around the world, by far the best known to North Americans is the destructive marine lamprey, *Petromyzon marinus,* of the Great Lakes (figure 16.4). The name *Petromyzon* (Gr. *petros,* stone, + *myzon,* sucking) refers to the lamprey's habit of grasping a stone with its mouth to hold position in a current. There are 22 species of lampreys in North America of which about half are parasitic; the rest are species that never feed after metamorphosis and die soon after spawning.

In North America all lampreys, marine as well as freshwater forms, spawn in the winter or spring in shallow gravel and sand in freshwater streams. Males begin nest building and are joined later by females. Using their oral discs to lift stones and pebbles and using vigorous body vibrations to sweep away light debris, they form an oval depression. As the female sheds eggs into the nest, they are fertilized by the male. The sticky eggs adhere to pebbles in the nest and soon become covered with sand. Adults die soon after spawning.

Eggs hatch in approximately 2 weeks, releasing small larvae (**ammocoetes**) (figure 16.5), which stay in the nest until they are approximately 1 cm long; they then burrow into mud or sand and emerge at night to feed on small invertebrates, detritus, and other particulate matter in the water. The larval period lasts from 3 to 7 or more years before the larva rapidly metamorphoses into an adult.

Parasitic lampreys either migrate to the sea, if marine, or remain in fresh water, where they attach themselves by their suckerlike mouth to fish and with their sharp horny teeth rasp through flesh and suck body fluids. To promote the flow of blood, a lamprey injects an anticoagulant into the wound. When gorged, a lamprey releases its hold but leaves the fish with a wound that may prove fatal. Parasitic freshwater adults live a year or more before spawning and then die; marine forms may live longer.

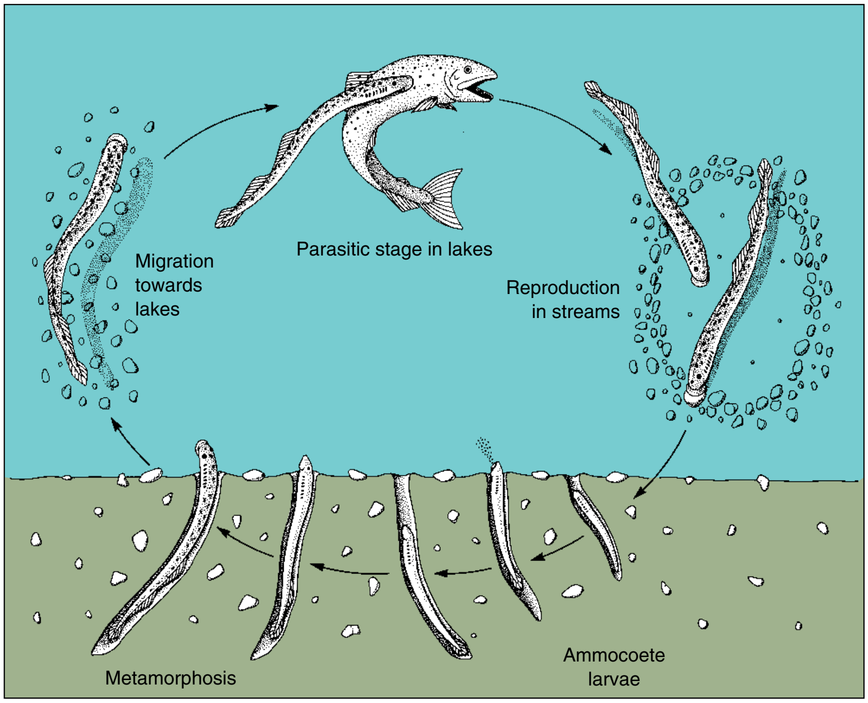


figure 16.5
Life cycle of the "landlocked" form of the sea lamprey *Petromyzon marinus*.

Nonparasitic lampreys do not feed after emerging as adults, since their alimentary canal degenerates to a nonfunctional strand of tissue. Within a few months and after spawning, they die.

The landlocked sea lamprey, *Petromyzon marinus* first entered the Great Lakes after the Welland Canal around Niagara Falls, a barrier to further western migration, was deepened between 1913 and 1918. Moving first through Lake Erie to Lakes Huron, Michigan, and Superior, sea lampreys, accompanied by overfishing, caused a total collapse of a multimillion dollar lake trout fishery in the early 1950s. Other less valuable fish species were attacked and destroyed in turn. After reaching a peak abundance in 1951 in Lakes Huron and Michigan and in 1961 in Lake Superior, sea lampreys began to decline, due in part to depletion of their food and in part to the effectiveness of control measures (mainly chemical larvicides placed in selected spawning streams). Lake trout, aided by a restocking program, are now recovering, but wounding rates are still high in some lakes. Fishery organizations are now experimenting with release into spawning streams of sterilized male lampreys; when fertile females mate with sterilized males, the female's eggs fail to develop.

Cartilaginous Fishes: Class Chondrichthyes

There are nearly 850 living species in the class Chondrichthyes, an ancient, compact, group. Although a much smaller and less diverse assemblage than bony fishes, their impressive combination of well-developed sense organs, powerful jaws and swimming musculature, and predaceous habits ensures them a secure and lasting niche in the aquatic community. One of their distinctive features is their cartilaginous skeleton. Although there is some limited calcification, bone is entirely absent throughout the class—a curious feature, since Chondrichthyes are derived from ancestors having well-developed bone.

Sharks and Rays: Subclass Elasmobranchii

Sharks, which make up about 45% of the approximately 815 species in subclass Elasmobranchii, are typically predaceous fishes with five to seven gill slits and gills on each side and (usually) a spiracle behind each eye. Sharks track their prey using their lateral line system and large olfactory organs, since their vision is not well developed. Larger sharks, such as the massive (but harmless) plankton-feeding whale shark, may reach 15 m in length, the largest of all fishes. Dogfish sharks, so widely used in zoological laboratories, rarely exceed 1 m. More than half of all elasmobranchs are rays, specialized for a bottom-feeding lifestyle. Unlike sharks, which swim with thrusts of the tail, rays propel themselves by wavelike motions of the "wings," or pectoral fins.

characteristics of sharks and rays (elasmobranchii)

1. **Body fusiform** (except rays) with a **heterocercal** caudal fin (figure 16.13)
2. **Mouth ventral** (figure 16.6); two olfactory sacs that do not connect to the mouth cavity; jaws present
3. Skin with **placoid scales** (figure 16.15) and mucous glands; teeth of modified placoid scales
4. **Endoskeleton entirely cartilaginous**
5. Digestive system with a J-shaped stomach and **intestine with spiral valve** (figure 16.7)
6. Circulatory system of several pairs of aortic arches; two-chambered heart
7. Respiration by means of 5 to 7 pairs of gills with **separate and exposed gill slits,** no operculum
8. No swim bladder or lung
9. Mesonephric kidney and rectal gland (figure 16.7); blood isosmotic or slightly hyperosmotic to seawater; **high concentrations of urea and trimethylamine oxide in blood**
10. Brain of two olfactory lobes, two cerebral hemispheres, two optic lobes, a cerebellum, and a medulla oblongata; 10 pairs of cranial nerves; **three pairs of semicircular canals;** senses of smell, vibration reception (lateral line system), and electroreception well developed
11. Separate sexes; oviparous, ovoviviparous, or viviparous; direct development; **internal fertilization**

Although to most people sharks have a sinister appearance and a fearsome reputation, they are at the same time among the most gracefully streamlined of all fishes (figure 16.6). Sharks are heavier than water and will sink if not swimming forward. The asymmetrical **heterocercal tail,** in which the vertebral column turns upward and extends into the dorsal lobe of the tail (see figure 16.13), provides lift and thrust as it sweeps to and fro in the water, and the broad head and flat pectoral fins act as planes to provide head lift.

Sharks are well equipped for their predatory life. Their tough leathery skin is covered with numerous dermal **placoid scales** (see figure 16.15) that are modified anteriorly to form replaceable rows of teeth in both jaws (figure 16.8). Placoid scales in fact consist of dentine enclosed by an enamel-like substance, and they very much resemble teeth of other vertebrates. Sharks have a keen sense of smell used to guide them to food. Vision is less acute than in most bony fishes, but a well-developed **lateral line system** is used for detecting and locating objects and moving animals (predators, prey, and social partners). It is composed of a canal system extending along the side of the body and over the head (figure 16.9). Inside are spe-

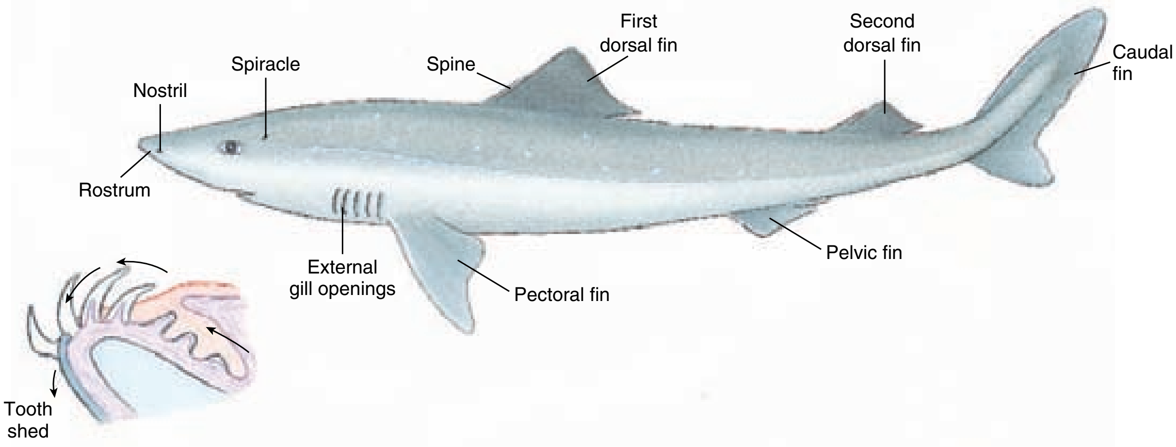


figure 16.6

Dogfish shark, *Squalus acanthias.* Inset: Section of lower jaw shows formation of new teeth developing inside the jaw. These move forward to replace lost teeth. Rate of replacement varies in different species.

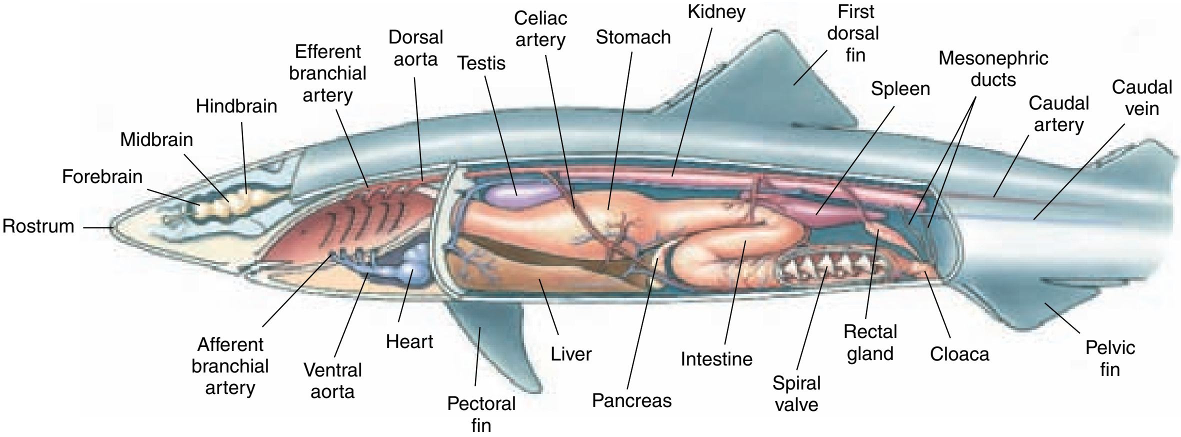


figure 16.7

Internal anatomy of dogfish shark *Squalus acanthias.*

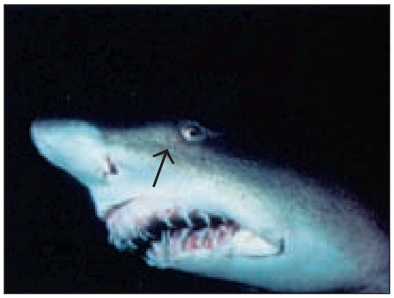


figure 16.8

Head of sand tiger shark *Carcharias* sp. Note the series of successional teeth. Also visible in a row below the eye are ampullae of Lorenzini (*arrow*).

cial receptor organs (**neuromasts**) that are extremely sensitive to vibrations and currents in the water. Sharks can also detect and aim attacks at prey buried in the sand by sensing the bioelectric fields that surround all animals. The receptors, the **ampullary organs of Lorenzini,** are located on the shark's head.

Rays belong to a separate order from sharks. Rays are distinguished by their dorsoventrally flattened bodies and the much-enlarged pectoral fins that behave as wings in swimming (figure 16.10). Gill openings are on the underside of the head, and the **spiracles** (on top of the head) are unusually large. Respiratory water enters through these spiracles to prevent clogging the gills, because the mouth is often buried in sand. Teeth are adapted for crushing prey—mainly molluscs, crustaceans, and an occasional small fish.

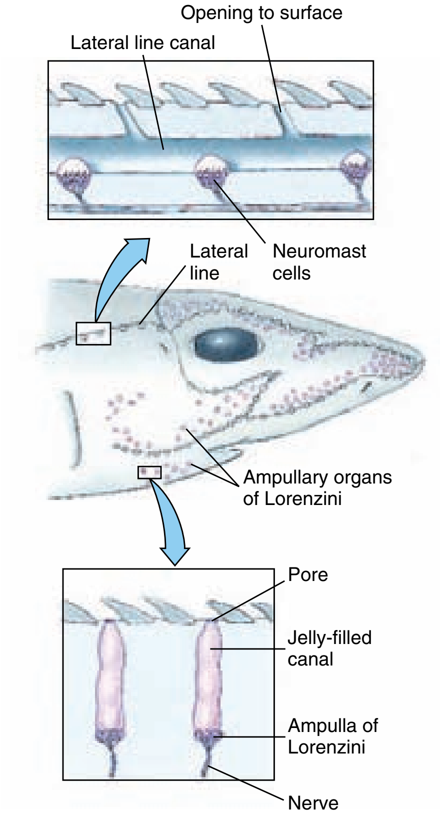


figure 16.9
Sensory canals and receptors in a shark. The ampullae of Lorenzini respond to weak electric fields, and possibly to temperature, water pressure, and salinity. Lateral line sensors, called neuromasts, are sensitive to disturbances in the water, enabling a shark to detect nearby objects by reflected waves in the water.

In stingrays, the caudal and dorsal fins have disappeared, and the tail is slender and whiplike. The stingray tail is armed with one or more saw-toothed spines that can inflict dangerous wounds. Electric rays have certain dorsal muscles modified into powerful electric organs, which can give severe shocks to stun their prey.

The worldwide shark fishery is experiencing unprecedented pressure, driven by the high price of shark fins for shark-fin soup, an oriental delicacy (which may sell for as much as $450.00 per bowl). Coastal shark populations in general have declined so rapidly that "finning" is to be outlawed in the United States; other countries, too, are setting quotas to protect threatened shark populations. Even in the Marine Resources Reserve of the Galápagos Islands, one of the world's exceptional wild places, tens of thousands of sharks have been killed illegally for the Asian shark-fin market. That illegal fishery continues at this writing. Contributing to the threatened collapse of shark fisheries worldwide is the long time required by most sharks to reach sexual maturity; some species take as long as 35 years.

In the order containing rays (Rajiformes), we commonly refer to members of one family (Rajidae) as skates. Alone among members of Rajiformes, skates do not bear living young but lay large, yolky eggs enclosed within a horny covering ("mermaid's purse") that often washes up on beaches. Although the tail is slender, skates have a somewhat more muscular tail than most rays, and they usually have two dorsal fins and sometimes a caudal fin.

Chimaeras: Subclass Holocephali

The approximately 30 species of chimaeras (ky-meer´uz; L. monster), distinguished by such suggestive names as ratfish (Figure 16.11), rabbitfish, spookfish, and ghostfish, are remnants of a group that diverged from the earliest shark lineage, which originated at least 360 million years ago (Devonian or Silurian periods of the Paleozoic). Fossil chimaeras first appeared in the Jurassic period, reached their zenith in the Cretaceous and early Tertiary periods (120 million to 50 million years ago), and have declined ever since. Anatomically they present an odd mixture of sharklike and bony fishlike features. Their food is a mixed diet of seaweed, molluscs, echinoderms, crustaceans, and fishes. Chimaeras are not commercial species and are seldom caught. Despite their grotesque shape, they are beautifully colored with a pearly iridescence.

figure 16.10
Skates and rays are specialized for life on the sea floor. Both the clearnose skate, *Raja eglanteria,* **A,** and the southern stingray, *Dasyatis americana,* **B,** are flattened dorsoventrally and move by undulations of winglike pectoral fins. This stingray, **B,** is followed by a pilot fish.

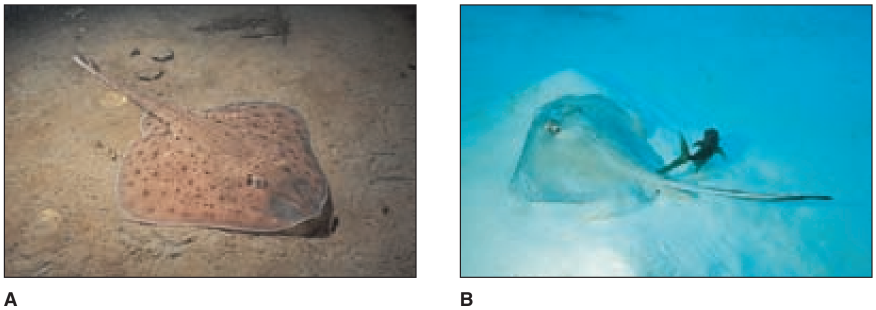


figure 16.11
Spotted ratfish, *Hydrolagus colliei,* of North American west coast. This species is one of the most handsome of chimaeras, which tend toward bizarre appearances.

characteristics of bony fishes (osteichthyes)

1. **Skeleton more or less bony,** vertebrae numerous; **tail usually homocercal** (figure 16.13)
2. Skin with mucous glands and embedded **dermal scales** (figure 16.14) of three types: **ganoid, cycloid,** or **ctenoid;** some without scales, no placoid scales (figure 16.15)
3. Fins both median and paired with **fin rays of cartilage or bone**
4. **Mouth terminal** with many teeth (some toothless); jaws present; olfactory sacs paired and may or may not open into mouth
5. Respiration by gills supported by bony gill arches and covered by a **common operculum**
6. **Swim bladder** often present with or without duct connected to pharynx
7. Circulation consisting of a two-chambered heart, arterial and venous systems, and four pairs of aortic arches
8. Nervous system of brain with small olfactory lobes and cerebrum; large optic lobes and cerebellum; 10 pairs of cranial nerves
9. Sexes separate (some hermaphroditic), gonads paired; fertilization usually external; larval forms may differ greatly from adults

Bony Fishes: The Osteichthyes Origin, Evolution, and Diversity

In the early to middle Silurian, a lineage of fishes with bony endoskeletons gave rise to a clade of vertebrates that contains 96% of living fishes and all living tetrapods. Fishes of this clade have traditionally been termed "bony fishes" (Osteichthyes), because it was originally believed these were the only fishes with bony skeletons. Although we know now that bone occurs in many other early fishes (ostracoderms, placoderms, and acanthodians), bony fishes and their tetrapod relatives are united by the presence of endochondral bone (bone that replaces cartilage developmentally), presence of lungs or a swim bladder derived embryonically from the gut, and several cranial and dental characters. Because the traditional usage of Osteichthyes does not describe a monphyletic (natural) group (see figure 16.2), most recent classifications, including the one presented at the end of this chapter, do not recognize this term as a valid taxon. Rather, it is used as a term of convenience to describe vertebrates with endochondral bone that are conventionally termed fishes.

Fossils of the earliest bony fishes show several structural similarities with acanthodians (p. 298 and figure 16.12), indicating that they likely descended from a common ancestor. By the middle of the Devonian bony fishes already had radiated extensively into two major lineages, with adaptations that fitted them for every aquatic habitat except the most inhospitable. One of these lineages, **ray-finned fishes** (class Actinopterygii), includes modern bony fishes (figure 16.12), the most speciose of living vertebrates. A second lineage, the **lobe-finned fishes** (class Sarcopterygii), is represented today only by lungfishes and coelacanths (see figures 16.18 and 16.19). The evolutionary history of this group is of particular interest because it gave rise to land vertebrates (tetrapods).

Several key adaptations contributed to their radiation. Bony fishes have an operculum over the gill composed of bony plates and attached to a series of muscles. This feature increased respiratory efficiency because outward rotation of the operculum created a negative pressure so that water would be drawn across the gills, as well as pushed across by the mouth pump. The earliest bony fishes also had a pair of lungs that provided an additional means of gas exchange in oxygen-poor waters and an efficient means of achieving neutral buoyancy. Progressive specialization of jaw musculature and skeletal elements involved in feeding is another key feature of bony fish evolution.

Ray-Finned Fishes: Class Actinopterygii

Ray-finned fishes are an enormous assemblage containing all of our familiar bony fishes—more than 24,600 species. The group had its beginnings in Devonian freshwater lakes and streams. The ancestral forms were small, bony fishes, heavily armored with ganoid scales (figure 16.15), and had functional lungs as well as gills.

From these earliest ray-finned fishes, two major groups emerged. Those bearing the most primitive characteristics are **chondrosteans** (Gr. *chondros,* cartilage, + *osteon,* bone), represented today by sturgeons, paddlefishes, and bichir *Polypterus* (Gr. *poly,* many, + *pteros,* winged) of African rivers (figure 16.16). *Polypterus* is an interesting relic with a lunglike swim bladder

figure 16.12

Internal anatomy of a yellow perch, *Perca flavescens*, a freshwater teleost fish.

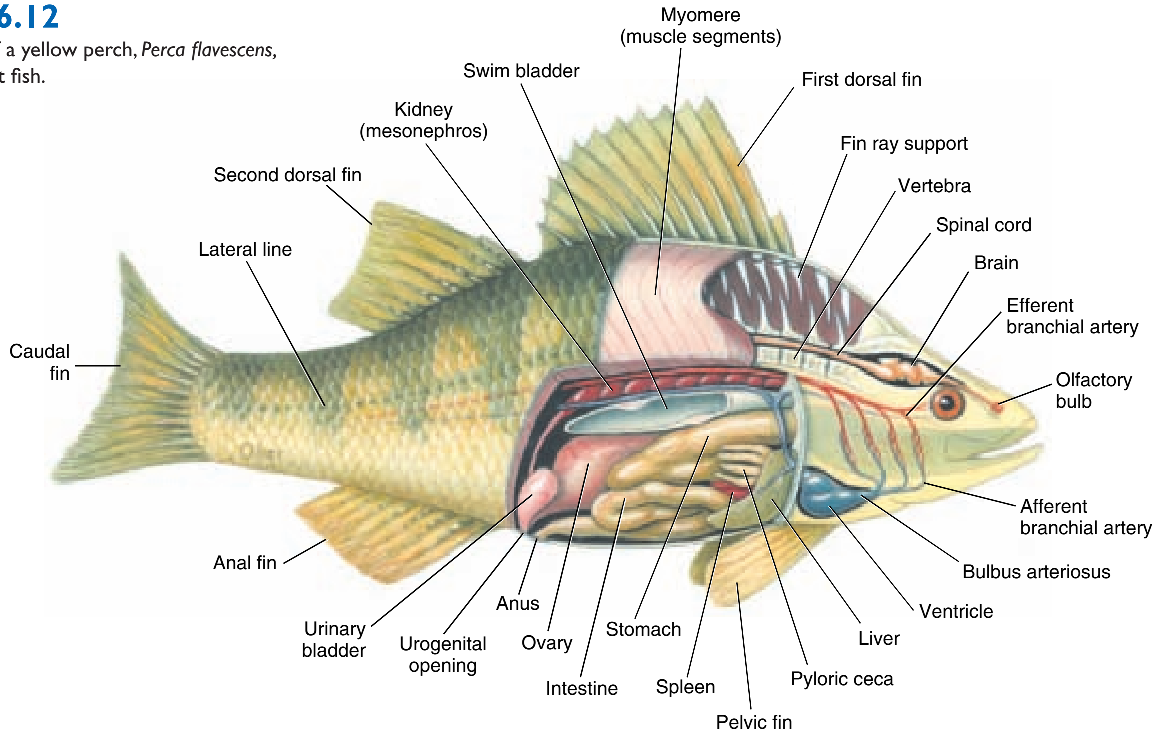
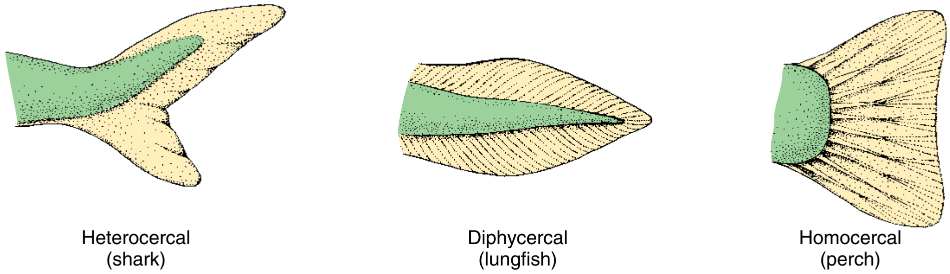


figure 16.13

Types of caudal fins among fishes.



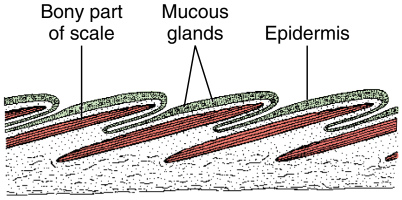


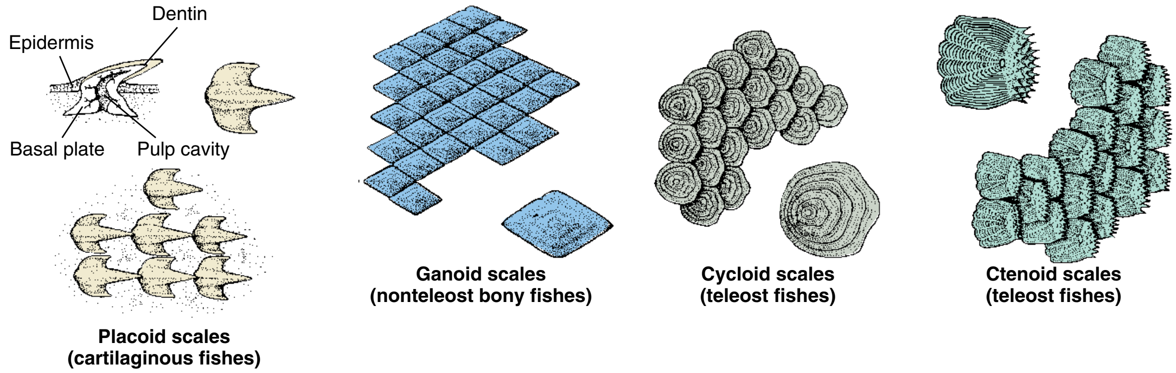
figure 16.14

Section through the skin of a bony fish, showing the overlapping scales (*red*). The scales lie in the dermis and are covered by epidermis.

and many other primitive characteristics; it resembles an ancestral ray-finned fish more than it does any other living descendant. There is no satisfactory explanation for the survival to the present of this fish and the coelacanth (*Latimeria*) when other species closely resembling them perished millions of years ago.

The second major group to emerge from the early ray-finned stock were **neopterygians** (Gr. *neos,* new, + *pteryx,* fin). Neopterygians appeared in the late Permian and radiated extensively during the Mesozoic era. During the Mesozoic one lineage gave rise to a secondary radiation that led to modern bony fishes, the teleosts. The two surviving genera of nonteleost neopterygians are the bowfin *Amia* (Gr. tunalike fish) of shallow, weedy waters of the Great Lakes and Mississippi Valley, and gars *Lepisosteus* (Gr. *lepidos,* scale, + *osteon,* bone) of eastern and southern North America (figure 16.17). Gars are large, ambush predators that belie their lethargic appearance by suddenly dashing forward to grasp their prey with needle-sharp teeth.

The major lineage of neopterygians is teleosts (Gr. *teleos,* perfect, + *osteon,* bone), the modern bony fishes (see figure 16.12). Diversity appeared early in teleost evolution, foreshadowing the truly incredible variety of body forms among teleosts today. Heavy armorlike scales of early ray-finned fishes have



Placoid scales (cartilaginous fishes)

Ganoid scales (nonteleost bony fishes)

Cycloid scales (teleost fishes)

Ctenoid scales (teleost fishes)

figure 16.15

Types of fish scales. Placoid scales are small, conical toothlike structures characteristic of Chondrichthyes. Diamond-shaped ganoid scales, present in gars and considered primitive for bony fishes, are composed of layers of silvery enamel (ganoin) on the upper surface and bone on the lower. Other bony fishes have either cycloid or ctenoid scales. These scales are thin and flexible and are arranged in overlapping rows.

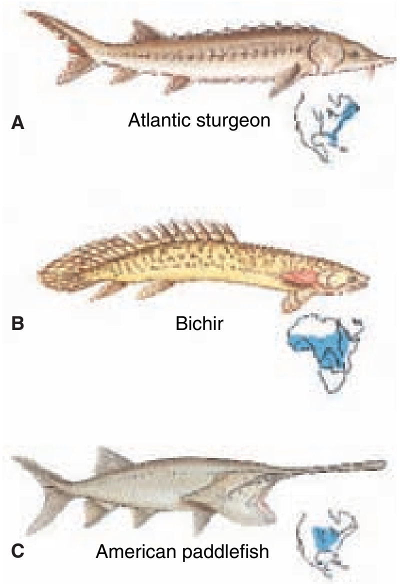


figure 16.16

Chondrostean ray-finned fishes of class Actinopterygii. **A,** Atlantic sturgeon, *Acipenser oxyrhynchus* (now uncommon) of Atlantic coastal rivers. **B,** Bichir, *Polypterus bichir,* of equatorial west Africa. It is a nocturnal predator. **C,** Paddlefish, *Polyodon spathula,* of the Mississippi River reaches a length of 2 m and a weight of 90 kg.

been replaced in teleosts by light, thin, and flexible **cycloid** and **ctenoid** scales (figure 16.15). Some teleosts, such as some catfishes and sculpins, lack scales altogether. Nearly all teleosts have a **homocercal tail,** with upper and lower lobes of about equal size (see figure 16.13). Lungs of early forms were transformed in teleosts to a swim bladder with a buoyancy function. Teleosts have highly maneuverable fins for control of body movement. In small teleosts fins are often provided with stout,

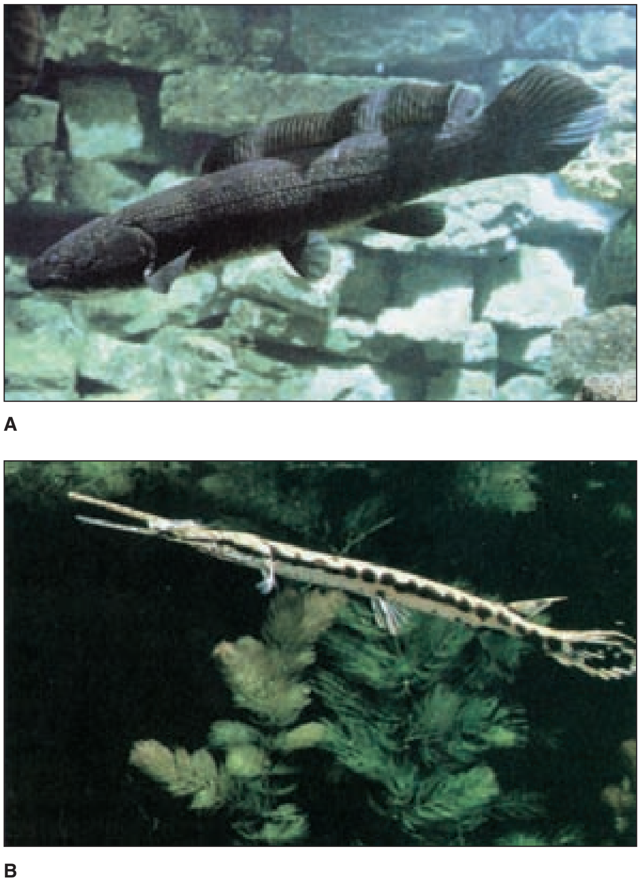


figure 16.17

Nonteleost neopterygian fishes. **A,** Bowfin *Amia calva.* **B,** Longnose gar *Lepisosteus osseus.* Bowfins live in the Great Lakes region and Mississippi basin. Gars are common fishes of eastern and southern North America. They frequent slow-moving streams where they may hang motionless in the water, ready to snatch passing fish.

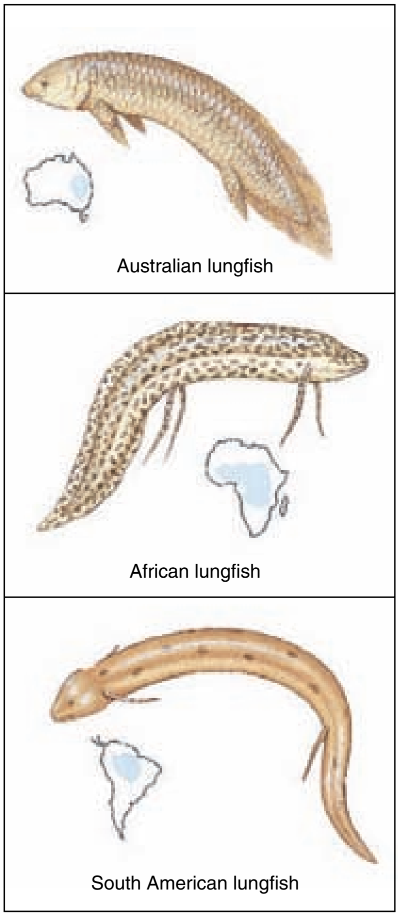
sharp spines, thus making themselves prickly mouthfuls for would-be predators. With these adaptations (and many others), teleosts have become the most diverse of fishes.

Lobe-Finned Fishes: Class Sarcopterygii

Lobe-finned fishes are today represented by only seven species: six species (three genera) of lungfishes and the coelacanth (seal'a-canth)—survivors of a group once abundant during the Devonian period of the Paleozoic. All early sarcopterygians had lungs as well as gills and strong, fleshy, paired lobed fins (pectoral and pelvic) that may have been used like four legs to scuttle along the bottom. They had powerful jaws, a skin covered with heavy, enameled scales, and a **diphycercal** tail (figure 16.13).

Neoceratodus (Gr. *neos,* new, + *keratos,* horn, + *odes,* form), the living Australian lungfish, may attain a length of 1.5 m (figure 16.18). This lungfish is able to survive in stagnant, oxygen-poor water by coming to the surface and gulping air into its single lung, but it cannot live out of water. The South American lungfish, *Lepidosiren* (L. *lepidus,* pretty, + *siren,* Siren, mythical mermaid), and the African lungfish, *Protopterus* (Gr. *protos,* first, + *pteron,* wing), can live out of water for long periods of time. *Protopterus* lives in African streams and rivers that are baked hard by the hot tropical sun during the dry season. The fish burrows down at the approach of the dry season and secretes a copious slime that mixes with mud to form a hard cocoon in which it remains dormant until the rains return.

Coelacanths and rhipidistians collectively have been termed crossopterygians, but this group is considered polyphyletic and no longer is recognized by most classifications. The **rhipidistians** flourished in the late Paleozoic era and then became extinct. Rhipidistians are of special importance because they include the ancestors of tetrapods (and, in cladistic terms, are therefore a paraphyletic group). **Coelacanths** also arose in the Devonian period, radiated somewhat, and reached their evolutionary peak in the Mesozoic era. At the end of the Mesozoic era they nearly disappeared but left one remarkable surviving species, *Latimeria chalumnae* (named for M. Courtenay-Latimer, South African museum director) (figure 16.19). Since the last coelacanths were believed to have become extinct 70 million years ago, the astonishment of the scientific world may be imagined when the remains of a coelacanth were found on a dredge off the coast of South Africa in 1938. An intensive search to locate more specimens was successful off the coast of the Comoro Islands. There fishermen occasionally catch them at great depths with hand lines, providing specimens for research. This was believed to be the only population of *Latimeria* until 1998, when the scientific


Australian lungfish

African lungfish

South American lungfish

figure 16.18

Lungfishes are lobe-finned fishes of Sarcopterygii. The African lungfish *Protopterus* is best adapted of the three for remaining dormant in mucous-lined cocoons breathing air during prolonged periods of drought.

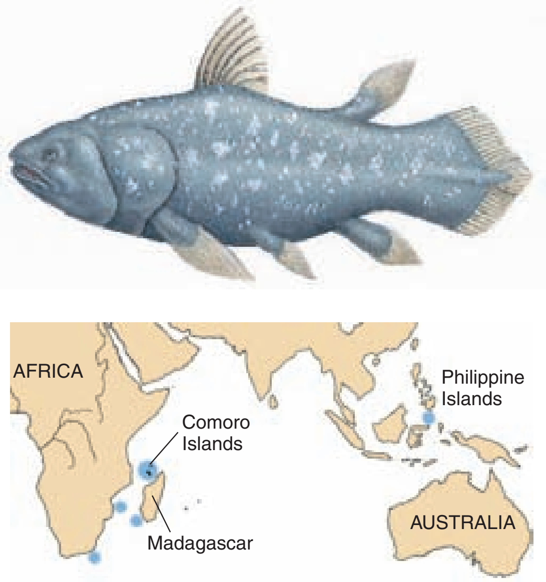


figure 16.19

The coelacanth *Latimeria chalumnae* is a surviving marine relict of a group of lobe-finned fishes that flourished some 350 million years ago.

world was again surprised by the capture of another coelacanth, possibly representing a new species, in Indonesia, 10,000 km from the Comoros!

The "modern" marine coelacanth is a descendant of the Devonian freshwater stock. The tail is of the diphycercal type (see figure 16.13) but possesses a small lobe between the upper and lower caudal lobes, producing a three-pronged structure (figure 16.19).

Coelacanths are a deep metallic blue with irregular white or brassy flecks, providing camouflage against the dark lava-cave reefs they inhabit. Young are born fully formed after hatching internally from eggs 9 cm in diameter—the largest among bony fishes.

Structural and Functional Adaptations of Fishes

Locomotion in Water

To the human eye, some fishes appear capable of swimming at extremely high speeds. But our judgment is unconsciously tempered by our own experience that water is a highly resistant medium through which to move. Most fishes, such as a trout or a minnow, can swim maximally about 10 body lengths per second, obviously an impressive performance by human standards. Yet when these speeds are translated into kilometers per hour it means that a 30 cm (1 foot) trout can swim only about 10.4 km (6.5 miles) per hour. As a general rule, the larger the fish the faster it can swim.

Measuring fish cruising speeds accurately is best done in a "fish wheel," a large ring-shaped channel filled with water that is turned at a speed equal and opposite to that of the fish. Much more difficult to measure are the sudden bursts of speed that most fish can make to capture prey or to avoid being captured. A hooked bluefin tuna was once "clocked" at 66 km per hour (41 mph); swordfish and marlin may be capable of incredible bursts of speed approaching, or even exceeding, 110 km per hour (68 mph). They can sustain such high speeds for no more than 1 to 5 seconds.

The propulsive mechanism of a fish is its trunk and tail musculature. The axial, locomotory musculature is composed of zigzag bands, called **myomeres.** Muscle fibers in each myomere are relatively short and connect the tough connective tissue partitions that separate each myomere from the next. On the surface myomeres take the shape of a W lying on its side (figure 16.20) but internally the bands are complexly folded and nested so that the pull of each myomere extends over several vertebrae. This arrangement produces more power and finer control of movement since many myomeres are involved in bending a given segment of the body.

Understanding how fishes swim can be approached by studying the motion of a very flexible fish such as an eel (figure 16.21). The movement is serpentine, not unlike that of a snake, with waves of contraction moving backward along the body by alternate contraction of the myomeres on either side. The anterior end of the body bends less than the posterior end, so that each undulation increases in amplitude as it travels along the body. While undulations move backward, bending of the body pushes laterally against the water, producing a **reactive force** that is directed forward, but at an angle. It can be analyzed as having two components: **thrust,** which is used to overcome drag and propels the fish forward, and **lateral force,** which tends to make the fish's head "yaw," or deviate from the course in the same direction as the tail. This side-to-side head movement is very obvious in a swimming eel or shark, but many fishes have a large, rigid head with enough surface resistance to minimize yaw.

Movement of an eel is reasonably efficient at low speed, but its body shape generates too much frictional drag for rapid swimming. Fishes that swim rapidly, such as trout, are less flexible and limit body undulations mostly to the caudal region (Figure 16.21). Muscle force generated in the large anterior muscle mass is transferred through tendons to the relatively nonmuscular caudal peduncle and tail where thrust is generated. This form of swimming reaches its highest development in tunas, whose bodies do not flex at all. Virtually all thrust is derived from powerful beats of the tail fin (figure 16.22). Many fast oceanic fishes such as marlin, swordfish, amberjacks, and wahoo have swept-back tail fins shaped much like a sickle. Such fins are the aquatic counterpart of the high-aspect ratio wings of the swiftest birds (p. 370–371). Swimming is the most economical form of animal locomotion, largely because aquatic animals are almost perfectly supported by their medium and need expend little energy to overcome the force of gravity.

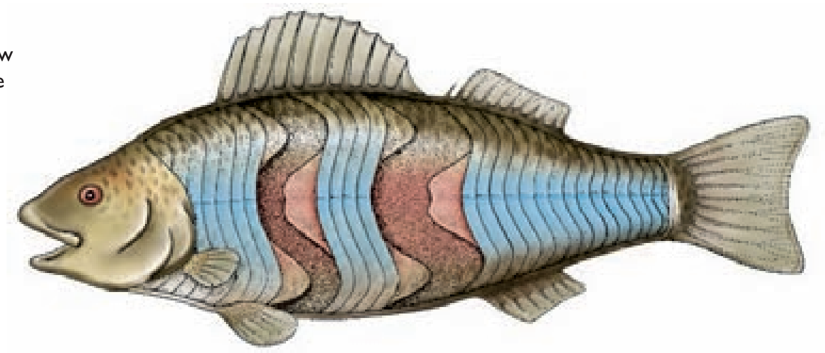
Neutral Buoyancy and the Swim Bladder

All fishes are slightly heavier than water because their skeletons and other tissues contain heavy elements that are present only in trace amounts in natural waters. To keep from sinking, sharks must always keep moving forward in the water. The asymmetrical (heterocercal) tail of a shark provides the necessary tail lift as it sweeps to and fro in the water, and the broad head and flat pectoral fins (see figure 16.6) act as angled planes to provide head lift. Sharks are also aided in buoyancy by having very large livers containing a special fatty hydrocarbon called **squalene,** which has a density of only 0.86. The liver thus acts like a large sack of buoyant oil that helps to compensate for a shark's heavy body.

By far the most efficient flotation device is a gas-filled space. **Swim bladders** are present in most pelagic bony fishes but are absent in tunas, most abyssal fishes, and most bottom dwellers, such as flounders and sculpins. By adjusting the volume of gas in its swim bladder, a fish can achieve neutral buoyancy and remain suspended indefinitely at any depth with no muscular effort. There are severe technical problems, however.

figure 16.20

Trunk musculature of a teleost fish, partly dissected to show internal arrangement of the muscle bands (myomeres). The myomeres are folded into a complex, nested grouping, an arrangement that favors stronger and more controlled swimming.



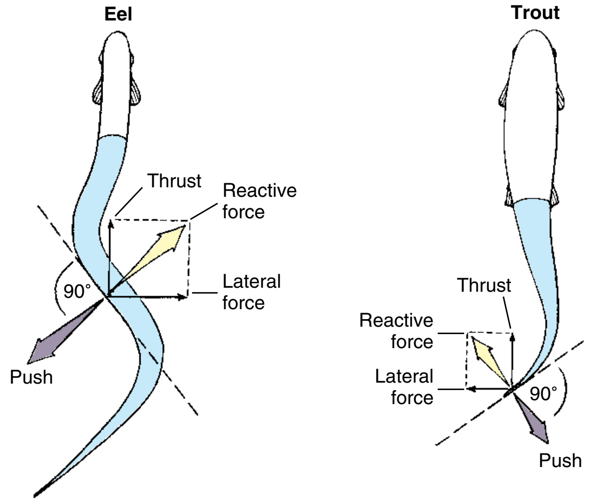


figure 16.21

Movements of swimming fishes, showing the forces developed by an eel-shaped and spindle-shaped fish.

Source: Vertebrate of Life, *4/e by Pough, et al., 1999. Reprinted by permission of Prentice-Hall, Inc., Upper Saddle River, NJ.*

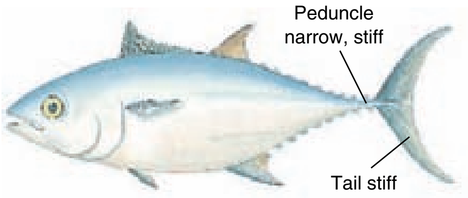


figure 16.22

Bluefin tuna, showing adaptations for fast swimming. Powerful trunk muscles pull on the slender tail stalk. Since the body does not bend, all of the thrust comes from beats of the stiff, sickle-shaped tail.

If a fish descends to a greater depth, its swim bladder gas is compressed so that the fish becomes heavier and tends to sink. Gas must be added to the bladder to establish a new equilibrium buoyancy. If a fish swims upward, the gas in the bladder expands, making the fish lighter. Unless gas is removed, the fish will rise with increasing speed while the bladder continues to expand.

Fishes adjust gas volume in their swim bladder in two ways. Some fishes (trout, for example) have a **pneumatic duct** that connects the swim bladder to the esophagus; these forms must come to the surface and gulp air to charge the bladder and obviously are restricted to relatively shallow depths. Other teleosts have lost the pneumatic duct. In these fishes, the gas must originate in the blood and be secreted into the swim bladder. Gas exchange depends on two highly specialized areas: a **gas gland** that secretes gas into the bladder and a **resorptive area,** or "ovale," that can remove gas from the bladder. The gas gland is supplied by a remarkable network of blood capillaries, called the **rete mirabile** ("marvelous net") that functions as a countercurrent exchange system to trap gases, especially oxygen, and prevent their loss to the circulation (figure 16.23).

The amazing effectiveness of this device is exemplified by a fish living at a depth of 2400 m (8000 feet). To keep the bladder inflated at that depth, the gas inside (mostly oxygen, but also variable amounts of nitrogen, carbon dioxide, argon, and even some carbon monoxide) must have a pressure exceeding 240 atmospheres, which is much greater than the pressure in a fully charged steel gas cylinder. Yet the oxygen pressure in the fish's blood cannot exceed 0.2 atmosphere—in equilibrium with the oxygen pressure in the atmosphere at the sea surface.

Respiration

Fish gills are composed of thin filaments, each covered with a thin epidermal membrane that is folded repeatedly into plate-like **lamellae** (figure 16.24). These are richly supplied with blood vessels. Gills are located inside a pharyngeal cavity and are covered with a movable flap, the **operculum.** This arrangement provides excellent protection to the delicate gill filaments, streamlines the body, and makes possible a pumping system for moving water through the mouth, across the gills, and out the operculum. Instead of opercular flaps as in bony fishes, elasmobranchs have a series of **gill slits** out of which the water flows. In both elasmobranchs and bony fishes the branchial mechanism is arranged to pump water continuously and smoothly over the gills, although to an observer it appears that fish breathing is pulsatile.

The flow of water is opposite to the direction of blood flow (countercurrent flow), the best arrangement for extracting the greatest possible amount of oxygen from water. Some bony fishes can remove as much as 85% of the dissolved oxygen from water passing over their gills. Very active fishes, such as herring and mackerel, can obtain sufficient water for their high oxygen demands only by swimming forward continuously to force water into their open mouth and across their gills. This process is called ram ventilation. Such fish will be asphyxiated if placed in an aquarium that restricts free swimming movements, even if the water is saturated with oxygen.

Migration

Eel

For centuries naturalists had been puzzled about the life history of freshwater eels, *Anguilla* (an-gwil´a) (L. eel), a common and commercially important species of coastal streams of the North Atlantic. Eels are **catadromous** (Gr. *kata,* down, + *dromos,* running), meaning that they spend most of their lives in fresh water but migrate to the sea to spawn. Each fall, people saw large numbers of eels swimming down rivers toward the sea, but no adults ever returned. Each spring countless numbers of young eels, called "elvers" (figure 16.25), each about the size of a wooden matchstick, appeared in coastal rivers and began swimming upstream. Beyond the assumption that eels must spawn somewhere at sea, the location of their breeding grounds was completely unknown.

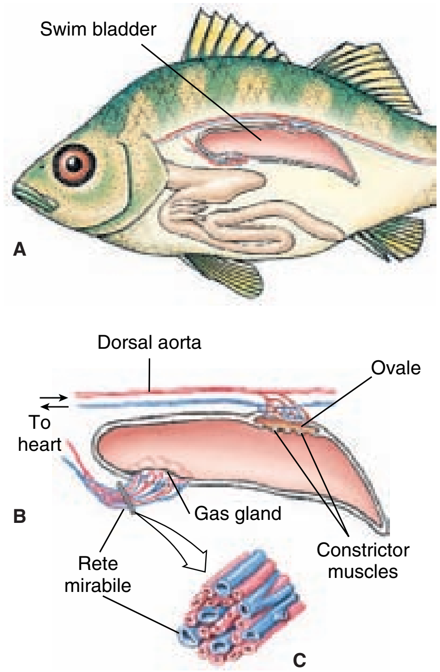


figure 16.23
A, Swim bladder of a teleost fish. The swim bladder lies in the coelom just beneath the vertebral column. **B,** Gas is secreted into the swim bladder by the gas gland. Gas from the blood is moved into the gas gland by the rete mirabile, a complex array of tightly-packed capillaries that act as a countercurrent multiplier to increase oxygen concentration. The arrangement of venous and arterial capillaries in the rete is shown in **C.** To release gas during ascent, a muscular valve opens, allowing gas to enter the ovale from which gas is removed by the circulation.

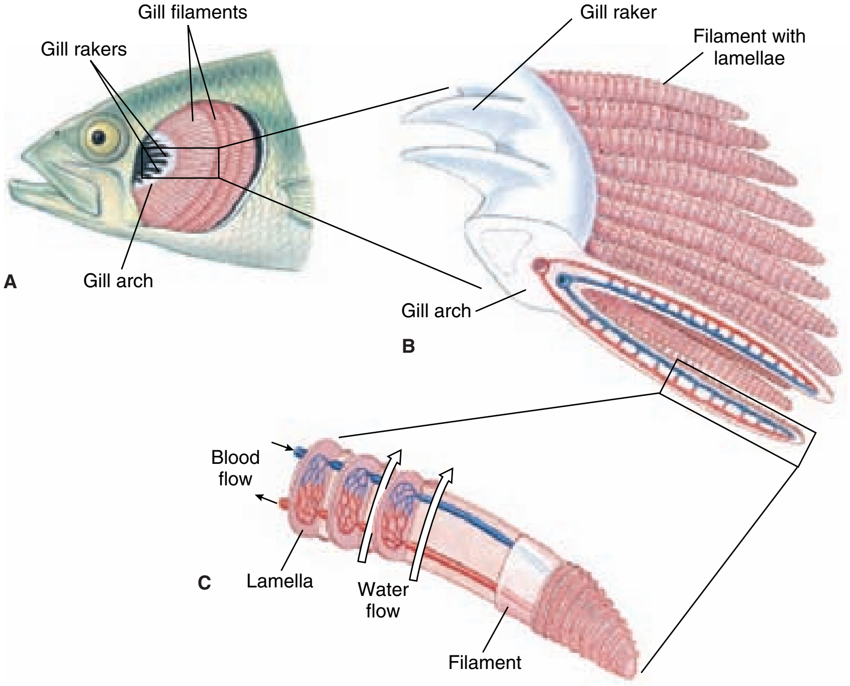


figure 16.24
Gills of fish. Bony, protective flap covering the gills (operculum) has been removed, **A,** to reveal branchial chamber containing the gills. There are four gill arches on each side, each bearing numerous filaments. A portion of gill arch, **B,** shows gill rakers that project forward to strain food and debris, and gill filaments that project to the rear. A single gill filament, **C,** is dissected to show the blood capillaries within the platelike lamellae. Direction of water flow (*large arrows*) is opposite the direction of blood flow.

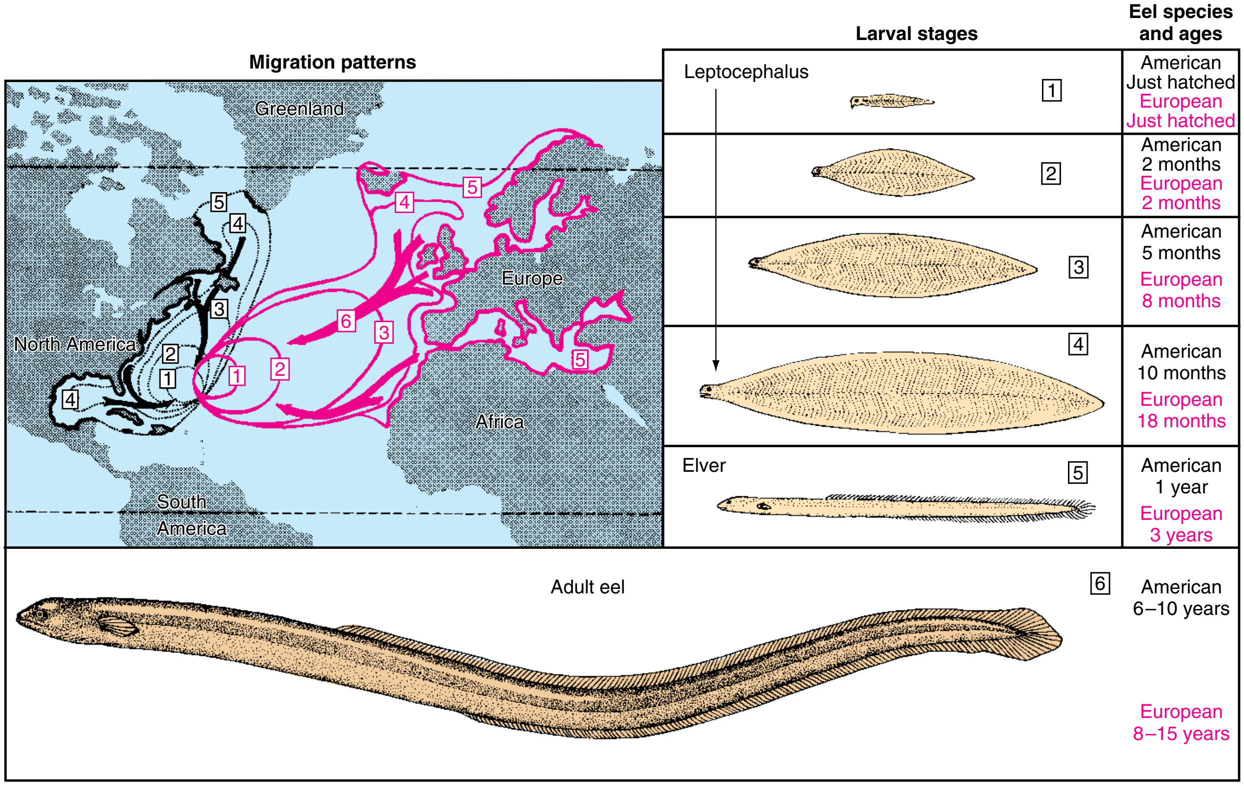


figure 16.25

Life histories of European eels, *Anguilla anguilla,* and American eels, *Anguilla rostrata. Red,* Migration patterns of European species. *Black,* Migration patterns of American species. Boxed numbers refer to stages of development. Note that American eels complete their larval metamorphosis and sea journey in one year. It requires nearly three years for European eels to complete their much longer journey.

The first clue was provided by two Italian scientists, Grassi and Calandruccio, who in 1896 reported that elvers were not larval eels but rather were relatively advanced juveniles. True larval eels, they discovered, were tiny, leaf-shaped, completely transparent creatures that bore absolutely no resemblance to an eel. They had been called **leptocephali** (Gr. *leptos,* slender, + *kephalē,* head) by early naturalists, who never suspected their true identity. In 1905 Johann Schmidt, supported by the Danish government, began a systematic study of eel biology that he continued until his death in 1933. With cooperation of captains of commercial vessels plying the Atlantic, thousands of leptocephali were caught in different areas of the Atlantic with plankton nets Schmidt supplied. By noting where larvae in different stages of development were captured, Schmidt and his colleagues eventually reconstructed the spawning migrations.

When adult eels leave the coastal rivers of Europe and North America, they swim steadily and apparently at great depth for one to two months until they reach the Sargasso Sea, a vast area of warm oceanic water southeast of Bermuda (figure 16.25). Here, at depths of 300 m or more, the eels spawn and die. Minute larvae then begin an incredible journey back to the coastal rivers of Europe. Drifting with the Gulf Stream, those not eaten by numerous predators reach the middle of the Atlantic after two years. By the end of the third year they reach the coastal waters of Europe where the leptocephali metamorphose into elvers, with an unmistakable eel-like body form (figure 16.25). Here males and females part company; males remain in the brackish waters of coastal rivers and estuaries while females continue up the rivers, often traveling hundreds of miles upstream. After 8 to 15 years of growth, females, now 1 m or more long, return to the sea to join the smaller males; both return to ancestral breeding grounds thousands of miles away to complete the life cycle. Since the Sargasso Sea is much closer to the American coastline than to Europe, American eel larvae require only about eight months to make their journey.

Recent enzyme electrophoretic analysis of eel larvae confirmed not only the existence of separate European and American species but also Schmidt's belief that the European and American eels spawn in partially overlapping areas of the Sargasso Sea.

Homing Salmon

The life history of salmon is nearly as remarkable as that of freshwater eels and certainly has received far more popular attention. Salmon are **anadromous** (Gr. *anadromous,* running upward); that is, they spend their adult lives at sea but return to fresh water to spawn. Atlantic salmon (*Salmo salar*) and Pacific salmon (six species of the genus *Oncorhynchus* [on-ko-rink'us]) have this practice, but there are important differences among the seven species. Atlantic salmon (as well as the closely related steelhead trout) make upstream spawning runs year after year. The six Pacific salmon species (king, sockeye, silver, humpback, chum, and Japanese masu) each make a single spawning run (figures 16.26 and 16.27), after which they die.

The virtually infallible homing instinct of the Pacific species is legendary. After migrating downstream as a smolt (a juvenile stage, figure 16.27), a sockeye salmon ranges many hundreds of miles over the Pacific for nearly four years, grows to 2 to 5 kg in weight, and then returns almost unerringly to spawn in the headwaters of its parent stream. Some straying does occur and is an important means of increasing gene flow and populating new streams.

Experiments by A. D. Hasler and others show that homing salmon are guided upstream by the characteristic odor of their parent stream. When salmon finally reach the spawning beds of their parents (where they themselves were hatched), they spawn and die. The following spring, newly hatched fry transform into smolts before and during the downstream migration. At this time they are imprinted with the distinctive odor of the stream, which is apparently a mosaic of compounds released by the characteristic vegetation and soil in the watershed of the parent stream. They also seem to imprint on odors of other streams they pass while migrating downriver and use these odors in reverse sequence as a map during the upriver migration as returning adults.

How do salmon find their way to the mouth of a coastal river from the trackless miles of open ocean? Salmon move hundreds of miles away from the coast, much too far to be able to detect the odor of their parent stream. Experiments suggest that some migrating fish, like birds, can navigate by orienting to the position of the sun. However, migrant salmon can navigate on cloudy days and at night, indicating that solar navigation, if used at all, cannot be a salmon's only navigational cue. Fish also (again, like birds, see p. 373) appear able to detect the earth's magnetic field and to navigate by orientating to it. Finally, fishery biologists concede that salmon may not require precise navigational abilities at all, but instead may use ocean currents, temperature gradients, and food availability to reach the general coastal area where "their" river is located. From this point, they would navigate by their imprinted odor map, making correct turns at each stream junction until they reach their natal stream.

figure 16.26
Migrating Pacific sockeye salmon.

Reproduction and Growth

In a group as diverse as fishes, it is no surprise to find extraordinary variations on the basic theme of sexual reproduction. Most fishes favor a simple theme: they are **dioecious,** with **external fertilization** and **external development** of their eggs and embryos. This mode of reproduction is called **oviparous** (meaning "egg-producing"). However, as tropical fish enthusiasts are well aware, the ever-popular guppies and mollies of home aquaria bear their young alive after development in the ovarian cavity of the mother (figure 16.28). These fish are said to be **ovoviviparous,** meaning "live egg-producing." Some sharks develop a kind of placental attachment through which the young are nourished during gestation. These forms, like placental mammals, are **viviparous** ("alive-producing").

Salmon runs in the Pacific Northwest have been devasted by a lethal combination of spawning stream degradation by logging, pollution and, especially, by more than 50 hydroelectric dams, which obstruct upstream migration of adult salmon and kill downstream migrants as they pass through the dams' power-generating turbines. In addition, the chain of reservoirs behind the dams, which has converted the Columbia and Snake Rivers into a series of lakes, increases mortality of young salmon migrating downstream by slowing their passage to the sea. The result is that the annual run of wild salmon is today only about 3% of the 10 to 16 million fish that ascended the rivers 150 years ago. While recovery plans have been delayed by the power industry, environmental groups argue that in the long run losing the salmon will be more expensive to the regional economy than making the changes now that will allow salmon stocks to recover.

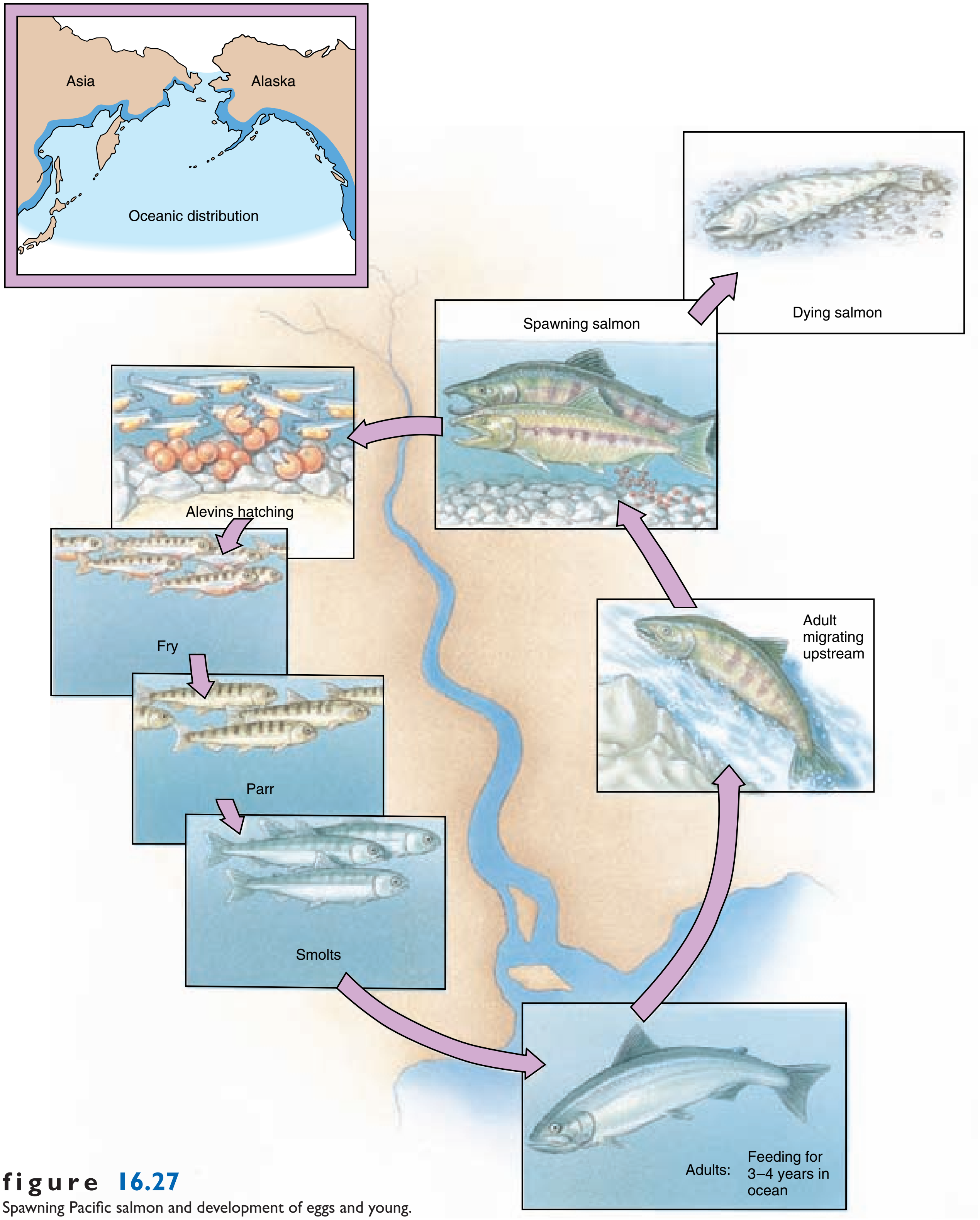


figure 16.27
Spawning Pacific salmon and development of eggs and young.

figure 16.28
Rainbow surfperch *Hypsurus caryi* giving birth. All of the West Coast surfperches (family Embiotocidae) are ovoviviparous.

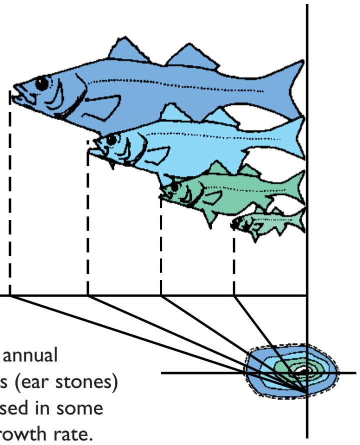


figure 16.30
Scale growth. Fish scales disclose seasonal changes in growth rate. Growth is interrupted during winter, producing year marks (annuli). Each year's increment in scale growth is a ratio to the annual increase in body length. Otoliths (ear stones) and certain bones can also be used in some species to determine age and growth rate.

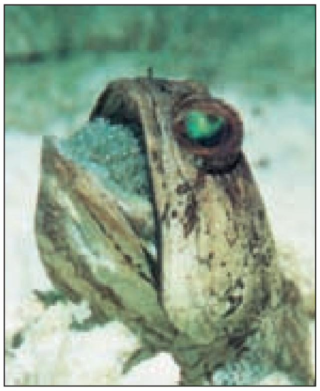


figure 16.29
Male banded jawfish *Opistognathus macrognathus* orally brooding its eggs. Males retrieve the female's spawn and incubate the eggs until they hatch. During brief periods when the jawfish is feeding, eggs are left in the burrow.

Let us return to the much more common oviparous mode of reproduction. Many marine fishes are extraordinarily profligate egg producers. Males and females aggregate in great schools and, without elaborate courtship behavior, release vast numbers of germ cells into the water to drift with currents. Large female cod may release 4 to 6 million eggs at a single spawning. Less than one in a million will survive the numerous perils of the ocean to reach reproductive maturity.

Unlike the minute, buoyant, transparent eggs of pelagic marine teleosts, those of many near-shore and bottom-dwelling (benthic) species are larger, typically yolky, nonbuoyant, and adhesive. Some bury their eggs, many attach them to vegetation, some deposit them in nests, and some even incubate them in their mouths (figure 16.29). Many benthic spawners guard their eggs. Intruders expecting an easy meal of eggs may be met with a vivid and often belligerent display by the guard, which is almost always the male.

Freshwater fishes almost invariably produce nonbuoyant eggs. Those, such as perch, that provide no parental care simply scatter their myriads of eggs among weeds or along the bottom. Freshwater fishes that do provide some form of egg care produce fewer, larger eggs that enjoy a better chance for survival.

Elaborate preliminaries to mating are the rule for freshwater fishes. A female Pacific salmon, for example, performs a ritualized mating "dance" with her breeding partner after arriving at the spawning bed in a fast-flowing, gravel-bottomed stream (see figure 16.27). She then turns on her side and scoops out a nest with her tail. As the eggs are laid by the female, they are fertilized by the male (see figure 16.27). After the female covers the eggs with gravel, the exhausted fish dies and drifts downstream.

Soon after an egg of an oviparous species is laid and fertilized, it takes up water and the outer layer hardens. Cleavage follows, and the blastoderm is formed, sitting astride a relatively enormous yolk mass. Soon the yolk mass is enclosed by developing blastoderm, which then begins to assume a fishlike shape. Many fishes hatch as larvae, carrying a semitransparent sac of yolk which provides its food supply until the mouth and digestive tract have developed. The larva then begins searching for its own food. After a period of growth a larva undergoes a metamorphosis, especially dramatic in many marine species such as freshwater eels described previously (see figure 16.25). Body shape is refashioned, fin and color patterns change, and it becomes a juvenile bearing the unmistakable definitive body form of its species.

Growth is temperature dependent. Consequently, fish living in temperate regions grow rapidly in summer when temperatures are high and food is abundant but nearly stop growing in winter. Annual rings in their scales reflect this seasonal growth (figure 16.30), a distinctive record of convenience to fishery biologists who wish to determine a fish's age. Unlike birds and mammals, which stop growing after reaching adult size, most fishes after attaining reproductive maturity continue to grow for as long as they live. This may be a selective advantage for the species, since the larger the fish, the more germ cells it produces and the greater its contribution to future generations.

classification of living fishes

The following Linnaean classification of major fish taxa mostly follows that of Nelson (1994). The probable relationships of these traditional groupings together with major extinct groups of fishes are shown in a cladogram in figure 16.2. Other schemes of classification have been proposed. Because of difficulty of determining relationships among the numerous living and fossil species, we can appreciate why fish classification has undergone, and will continue to undergo, continuous revision.

Phylum Chordata

Subphylum Vertebrata (Craniata)

Superclass Agnatha (ag´na-tha) (Gr. *a,* not, + *gnathos,* jaw) **(Cyclostomata).** No jaws; cartilaginous skeleton; paired limbs absent; one or two semicircular canals; notochord persistent. A paraphyletic group that is retained because of traditional usage.

Class Myxini (mik-sy´ny) (Gr. *myxa,* slime): hagfishes. Mouth terminal with four pairs of tentacles; nasal sac with duct to pharynx; 5 to 15 pairs of gill pouches; partially hermaphroditic.

Class Cephalaspidomorphi (sef-a-lass´pe-do-morf´e) (Gr. *kephalē,* head, + aspidos, shield, + *morphē,* form) **(Petromyzontes): lampreys.** Mouth suctorial with horny teeth; nasal sac not connected to mouth; seven pairs of gill pouches.

Superclass Gnathostomata (na´tho-sto´ma-ta) (Gr. *gnathos,* jaw, + *stoma,* mouth). Jaws present; usually paired limbs; three pairs of semicircular canals; notochord partly or completely replaced by vertebral centra. A paraphyletic group.

Class Chondrichthyes (kon-drik´thee-eez) (Gr. *chondros,* cartilage, + *ichthys,* fish): **cartilaginous fishes.** Cartilaginous skeleton; teeth not fused to jaws; no swim bladder; intestine with spiral valve.

Subclass Elasmobranchii (e-laz´mo-bran´kee-i) (Gr. *elasmos,* plated, + *branchia,* gills): **sharks and rays.** Placoid scales or no scales; 5 to 7 gill arches and gills in separate clefts along pharynx. Examples: Squalus, Raja.

Subclass Holocephali (hol´o-sef´a-li) (Gr. *holos,* entire, + *kephalē,* head): **chimaeras,** or **ghostfish.** Gill slits covered with operculum; jaws with tooth plates; single nasal opening; without scales; accessory clasping organs in male; lateral line an open groove.

Class Actinopterygii (ak´ti-nop-te-rij´ee-i) (Gr. *aktis,* ray, + *pteryx,* fin, wing): **ray-finned fishes.** Skeleton ossified; single gill opening covered by operculum; paired fins supported primarily by dermal rays; limb musculature within body; swim bladder, if present, mainly a hydrostatic organ.

Subclass Chondrostei (kon-dros´tee-i) (Gr. *chondros,* cartilage, + *osteon,* bone): **chondrostean ray-finned fishes.** Skeleton primarily cartilage; caudal fin heterocercal; scales ganoid, if present; more fin rays than ray supports. Two living orders containing the bichir (*Polypterus*), sturgeons, and paddlefish.

Subclass Neopterygii (nee-op-te-rij´ee-i) (Gr. *neos,* new, + *pteryx,* fin, wing): **modern bony fishes.** Skeleton primarily bone; caudal fin usually homocercal; scales cycloid, ctenoid, absent, or rarely, ganoid; fin ray number equal to their supports in dorsal and anal fins. Living neopterygeans are broadly divided into nonteleosts, two orders represented by gars (*Lepisosteus*) and the bowfin (*Amia*) ("holosteans" in older classifications); and teleosts, represented by 38 living orders. There are approximately 23,640 living named species of neopterygians (96% of all living fishes).

Class Sarcopterygii (sar-cop-te-rij´ee-i) (Gr. *sarkos,* flesh, + *pteryx,* fin, wing): **lobe-finned fishes.** Heavy bodied; paired fins with sturdy internal skeleton of basic tetrapod type and musculature; muscular lobes at bases of anal and second dorsal fins; diphycercal tail; intestine with spiral valve. Ten extinct orders and three living orders containing the coelacanth, Latimeria chalumnae, and three genera of lungfishes: Neoceratodus, Lepidosiren, and Protopterus. Not a monophyletic group unless tetrapods are included.

summary

Fishes are poikilothermic, gill-breathing aquatic vertebrates with fins. They include the oldest vertebrate groups, having originated from an unknown chordate ancestor in the Cambrian period or possibly earlier. Five classes of fishes are recognized. Jawless hagfishes (class Myxini) and lampreys (class Cephalaspidomorphi) are remnant groups having an eel-like body form without paired fins; a cartilaginous skeleton (although their ancestors, the ostracoderms, had bony skeletons); a notochord that persists throughout life; and a disclike mouth adapted for sucking or biting. All other vertebrates have jaws, a major development in vertebrate evolution.

Members of the class Chondrichthyes (sharks, rays, and chimaeras) are a compact group having a cartilaginous skeleton (a derived feature), paired fins, excellent sensory equipment, and an active, characteristically predaceous habit. Bony fishes (Osteichthyes), which may be divided into two classes. One is a relict group, lobe-finned fishes of class Sarcopterygii, represented today by lungfishes and the coelacanth. Terrestrial vertebrates arose from within one lineage of this group. The second is ray-finned fishes (class Actinopterygii), a huge and diverse modern assemblage containing most freshwater and marine fishes.

Modern bony fishes (teleost fishes) have radiated into approximately 23,600 species that reveal an enormous diversity of adaptations, body form, behavior, and habitat preference. Most fishes swim by undulatory contractions of their body muscles, which generate thrust (propulsive force) and lateral force. Flexible fishes oscillate the whole body, but in more rapid swimmers the undulations are limited to the caudal region or tail fin alone.

Most pelagic bony fishes achieve neutral buoyancy in water using a gas-filled swim bladder, the most effective gas-secreting device known in the animal kingdom. Gills of fishes, having efficient countercurrent flow between water and blood, facilitate high rates of oxygen exchange.

Many fishes are migratory to some extent, and some, such as freshwater eels and anadromous salmon, make remarkable migrations of great length and precision. Fishes reveal an extraordinary range of sexual reproductive strategies. Most fishes are oviparous, but ovoviviparous and viviparous fishes are not uncommon. Reproductive investment may be in large numbers of germ cells with low survival (many marine fishes) or in fewer germ cells with greater parental care for better survival (many freshwater fishes).

review questions

1. Provide a brief description of fishes citing characteristics that would distinguish them from all other animals.
2. What characteristics distinguish hagfishes and lampreys from all other fishes?
3. Describe feeding behavior in hagfishes and lampreys. How do they differ?
4. Describe the life cycle of the sea lamprey, *Petromyzon marinus,* and the history of its invasion of the Great Lakes.
5. In what ways are sharks well equipped for a predatory life habit?
6. The lateral line system has been described as a "distant touch" system for sharks. What function does the lateral line system serve? Where are the receptors located?
7. Explain how bony fishes differ from sharks and rays in the following systems or features: skeleton, tail shape, scales, buoyancy, respiration, and reproduction.
8. Match the ray-finned fishes in the right column with the group to which each belongs in the left column:

___ Chondrosteans	a. Perch
___ Nonteleost neopterygians	b. Sturgeon
	c. Gar
___ Teleosts	d. Salmon
	e. Paddlefish
	f. Bowfin

9. Although chondrosteans are today a relict group, they were one of two major lineages that emerged from early ray-finned fishes of the Devonian period. Give examples of living chondrosteans. What does the term Actinopterygii, the class to which the chondrosteans belong, literally mean (refer to the Classification of living fishes on p. 322)?
10. What is the other major group of actinopterygians? What are some distinguishing characteristics of modern bony fishes?
11. Only seven species of lobe-finned fishes are alive today, remnants of a group that flourished in the Devonian period of the Paleozoic. What morphological characteristics distinguish lobe-finned fishes? What is the literal meaning of Sarcopterygii, the class to which the lobe-finned fishes belong?
12. Give the geographical locations of the three surviving genera of lungfishes and explain how they differ in their ability to survive out of water.
13. Describe the discovery of the living coelacanth. What is the evolutionary significance of the group to which it belongs?
14. Compare the swimming movements of eels with those of trout, and explain why the latter are more efficient for rapid locomotion.
15. Sharks and bony fishes approach or achieve neutral buoyancy in different ways. Describe the methods evolved in each group. Why must a teleost fish adjust the gas volume in its swim bladder when it swims upward or downward? How is gas volume adjusted?
16. What is meant by "countercurrent flow" as it applies to fish gills?
17. Describe the life cycle of European eels. How does the life cycle of American eels differ from that of the European?
18. How do adult Pacific salmon find their way back to their parent stream to spawn?
19. What mode of reproduction in fishes is described by each of the following terms: oviparous, ovoviviparous, viviparous?
20. Reproduction in marine pelagic fishes and in freshwater fishes is distinctively different. How and why do they differ?

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See also general references on page 406.

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