evolutionary heritage. Thus, we now have the nonavian reptiles and the avian reptiles in our reptilian classification. We consider them separately only for convenience. Further, we will consider hagfishes and lampreys together as jawless fishes, the **Agnatha**, although emerging classification schemes separate them into chordate jawless fishes (the hagfishes) and vertebrate jawless fishes (the lampreys).

Animals that possess jaws are known as **gnathostomes**, which means "jawed mouth." Gnathostomes include fishes and tetrapods. **Tetrapod** literally means "four-footed," which refers to the phylogenetic history of various land vertebrates, even though in some of the tetrapods, the limbs may have been modified for purposes other than walking. Tetrapods include amphibians, reptiles, birds, and mammals, and technically could also refer to the extinct fishlike groups that gave rise to the tetrapods. Tetrapods can be further divided into two groups: amphibians and amniotes. Amniotes are animals whose eggs contain four extraembryonic membranes (yolk sac, amnion, chorion, and allantois) that provide nutrition and a water-retaining environment for their embryos. Amniotes are adapted for terrestrial living, and include mammals, reptiles, and birds.

# 29.2 Fishes

*By the end of this section, you will be able to do the following:*

- Describe the difference between jawless and jawed fishes
- Discuss the distinguishing features of sharks and rays compared to other modern fishes

Modern fishes include an estimated 31,000 species, by far the most of all clades within the Vertebrata. Fishes were the earliest vertebrates, with jawless species being the earliest forms and jawed species evolving later. They are active feeders, rather than sessile, suspension feeders. The Agnatha (jawless fishes)—the hagfishes and lampreys—have a distinct cranium and complex sense organs including eyes, that distinguish them from the invertebrate chordates, the urochordates and cephalochordates.

## Jawless Fishes: Superclass Agnatha

Jawless fishes (Agnatha) are craniates representing an ancient vertebrate lineage that arose over 550 million years ago. In the past, hagfishes and lampreys were sometimes recognized as separate clades within the Agnatha, primarily because lampreys were regarded as true vertebrates, whereas hagfishes were not. However, recent molecular data, both from rRNA and mtDNA, as well as embryological data, provide strong support for the hypothesis that living agnathans—previously called *cyclostomes*—are monophyletic, and thus share recent common ancestry. The discussion below, for convenience, separates the modern "cyclostomes" into the class Myxini and class Petromyzontida. The defining features of the living jawless fishes are the lack of jaws and lack of paired lateral appendages (fins). They also lack internal ossification and scales, although these are not defining features of the clade.

Some of the earliest jawless fishes were the armored ostracoderms (which translates to "shell-skin"): vertebrate fishes encased in bony armor—unlike present-day jawless fishes, which lack bone in their scales. Some ostracoderms, also unlike living jawless fishes, may have had paired fins. We should note, however, that the "ostracoderms" represent an assemblage of heavily armored extinct jawless fishes that may not form a natural evolutionary group. Fossils of the genus *Haikouichthys* from China, with an age of about 530 million years, show many typical vertebrate characteristics including paired eyes, auditory capsules, and rudimentary vertebrae.

### Class Myxini: Hagfishes

The class **Myxini** includes at least 70 species of hagfishes—eel-like scavengers that live on the ocean floor and feed on living or dead invertebrates, fishes, and marine mammals (Figure 29.9). Although they are almost completely blind, sensory barbels around the mouth help them locate food by smell and touch. They feed using keratinized teeth on a movable cartilaginous plate in the mouth, which rasp pieces of flesh from their prey. These feeding structures allow the gills to be used exclusively for respiration, *not* for filter feeding as in the urochordates and cephalochordates. Hagfishes are entirely marine and are found in oceans around the world, except for the polar regions. Unique slime glands beneath the skin release a milky mucus (through surface pores) that upon contact with water becomes incredibly slippery, making the animal almost impossible to hold. This slippery mucus thus allows the hagfish to escape from the grip of predators. Hagfish can also twist their bodies into a knot, which provides additional leverage to feed. Sometimes hagfish enter the bodies of dead animals and eat carcasses from the inside out! Interestingly, they do not have a stomach!

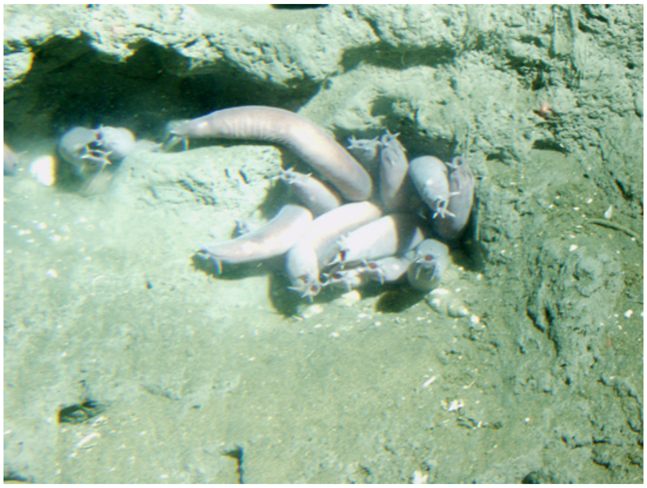

Figure 29.9 Hagfish. Pacific hagfish are scavengers that live on the ocean floor. (credit: Linda Snook, NOAA/CBNMS)

Hagfishes have a cartilaginous skull, as well as a fibrous and cartilaginous skeleton, but the major supportive structure is the notochord that runs the length of the body. In hagfishes, the notochord is *not* replaced by the vertebral column, as it is in true vertebrates, and thus they may (morphologically) represent a sister group to the true vertebrates, making them the most basal clade among the skull-bearing chordates.

## Class Petromyzontida: Lampreys

The class **Petromyzontida** includes approximately 40 species of lampreys, which are superficially similar to hagfishes in size and shape. However, lampreys possess extrinsic eye muscles, at least two semicircular canals, and a true cerebellum, as well as simple vertebral elements, called *arcualia*—cartilaginous structures arranged above the notochord. These features are also shared with the *gnathostomes*—vertebrates with jawed mouths and paired appendages (see below). Lampreys also have a dorsal tubular nerve cord with a well-differentiated brain, a small cerebellum, and 10 pairs of nerves. The classification of lampreys is still debated, but they clearly represent one of the oldest divergences of the vertebrate lineage. Lampreys lack paired appendages, as do the hagfishes, although they have one or two fleshy dorsal fins. As adults, lampreys are characterized by a rasping tongue within a toothed, funnel-like sucking mouth. Many species have a parasitic stage of their life cycle during which they are fish ectoparasites (some call them predators because they attack and eventually fall off) (Figure 29.10).

Figure 29.10 Lamprey. These parasitic sea lampreys, *Petromyzon marinus,* attach by suction to their lake trout host, and use their rough tongues to rasp away flesh in order to feed on the trout's blood. (credit: USGS)

Lampreys live primarily in coastal and freshwater environments, and have a worldwide distribution, except for the tropics and polar regions. Some species are marine, but all species spawn in fresh water. Interestingly, northern lampreys in the family Petromyzontidae, have the highest number of chromosomes (164 to 174) among the vertebrates. Eggs are fertilized externally, and the larvae (called *ammocoetes*) differ greatly from the adult form, closely resembling the adult cephalocordate *amphioxus*. After spending three to 15 years as suspension feeders in rivers and streams, they attain sexual maturity. Shortly afterward, the adults swim upstream, reproduce, and die within days.

## Gnathostomes: Jawed Fishes

**Gnathostomes**, or "jaw-mouths," are vertebrates that possess true jaws—a milestone in the evolution of the vertebrates. In fact, one of the most significant developments in early vertebrate evolution was the development of the jaw: a hinged structure attached to the cranium that allows an animal to grasp and tear its food. Jaws were probably derived from the first pair of gill arches supporting the gills of jawless fishes.

Early gnathostomes also possessed two sets of paired fins, allowing the fishes to maneuver accurately. Pectoral fins are typically located on the anterior body, and pelvic fins on the posterior. Evolution of the jaw and paired fins permitted gnathostomes to expand their food options from the scavenging and suspension feeding of jawless fishes to active predation. The ability of gnathostomes to exploit new nutrient sources probably contributed to their replacing most jawless fishes during the Devonian period. Two early groups of gnathostomes were the *acanthodians* and *placoderms* (Figure 29.11), which arose in the late Silurian period and are now extinct. Most modern fishes are gnathostomes that belong to the clades Chondrichthyes and Osteichthyes (which include the class Actinoptertygii and class Sarcopterygii).

**Figure 29.11** A placoderm. *Dunkleosteus* was an enormous placoderm from the Devonian period, 380 to 360 million years ago. It measured up to 10 meters in length and weighed up to 3.6 tons. Its head and neck were armored with heavy bony plates. Although *Dunkleosteus* had no true teeth, the edge of the jaw was armed with sharp bony blades. (credit: Nobu Tamura)

### Class Chondrichthyes: Cartilaginous Fishes

The class Chondrichthyes (about 1,000 species) is a morphologically diverse clade, consisting of subclass Elasmobranchii (sharks [Figure 29.12], rays, and skates, together with the obscure and critically endangered sawfishes), and a few dozen species of fishes called *chimaeras*, or "ghost sharks" in the subclass Holocephali. Chondrichthyes are jawed fishes that possess paired fins and a skeleton made of cartilage. This clade arose approximately 370 million years ago in the early or middle Devonian. They are thought to be descended from the placoderms, which had endoskeletons made of bone; thus, the lighter cartilaginous skeleton of Chondrichthyes is a secondarily derived evolutionary development. Parts of shark skeleton are strengthened by granules of calcium carbonate, but this is not the same as bone.

Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for a part or all of their lives. Most sharks are carnivores that feed on live prey, either swallowing it whole or using their jaws and teeth to tear it into smaller pieces. Sharks have abrasive skin covered with tooth-like scales called placoid scales. Shark teeth probably evolved from rows of these scales lining the mouth. A few species of sharks and rays, like the enormous whale shark (Figure 29.13), are suspension feeders that feed on plankton. The sawfishes have an extended rostrum that looks like a double-edged saw. The rostrum is covered with electrosensitive pores that allow the sawfish to detect slight movements of prey hiding in the muddy sea floor. The teeth in the rostrum are actually modified tooth-like structures called denticles, similar to scales.

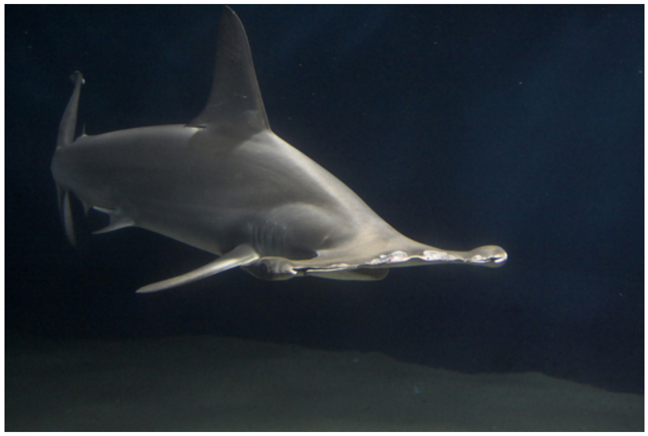

**Figure 29.12** Shark. Hammerhead sharks tend to school during the day and hunt prey at night. (credit: Masashi Sugawara)

Sharks have well-developed sense organs that aid them in locating prey, including a keen sense of smell and the ability to detect electromagnetic fields. Electroreceptors called **ampullae of Lorenzini** allow sharks to detect the electromagnetic fields that are produced by all living things, including their prey. (Electroreception has only been observed in aquatic or amphibious animals and sharks have perhaps the most sensitive electroreceptors of any animal.) Sharks, together with most fishes and aquatic and larval amphibians, also have a row of sensory structures called the **lateral line**, which is used to detect movement and vibration in the surrounding water, and is often considered to be functionally similar to the sense of "hearing" in terrestrial vertebrates. The lateral line is visible as a darker stripe that runs along the length of a fish's body. Sharks have no mechanism for maintaining neutral buoyancy and must swim continuously to stay suspended in the water. Some must also swim in order to ventilate their gills but others have muscular pumps in their mouths to keep water flowing over the gills.

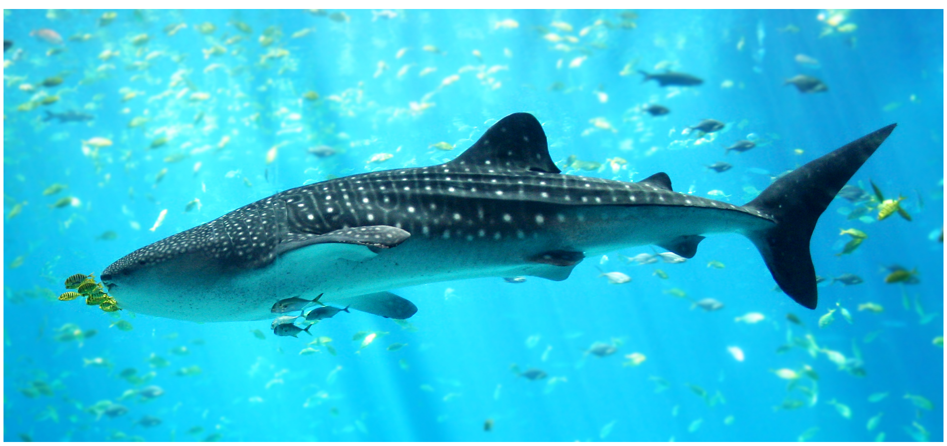

**Figure 29.13** Whale shark in the Georgia Aquarium. Whale sharks are filter-feeders and can grow to be over 10 meters long. Whale sharks, like most other sharks, are ovoviviparous. (credit: modified from Zac Wolf [Own work] [CC BY-SA 2.5 (http://creativecommons.org/licenses/by-sa/2.5 (http://openstax.org/l/CCSA) )], via Wikimedia Commons)

Sharks reproduce sexually, and eggs are fertilized internally. Most species are *ovoviviparous*: The fertilized egg is retained in the oviduct of the mother's body and the embryo is nourished by the egg yolk. The eggs hatch in the uterus, and young are born alive and fully functional. Some species of sharks are oviparous: They lay eggs that hatch outside of the mother's body. Embryos are protected by a shark egg case or "mermaid's purse" (Figure 29.14) that has the consistency of leather. The shark egg case has tentacles that snag in seaweed and give the newborn shark cover. A few species of sharks, e.g., tiger sharks and hammerheads, are viviparous: the yolk sac that initially contains the egg yolk and transfers its nutrients to the growing embryo becomes attached to the oviduct of the female, and nutrients are transferred directly from the mother to the growing embryo. In both viviparous and ovoviviparous sharks, gas exchange uses this yolk sac transport.

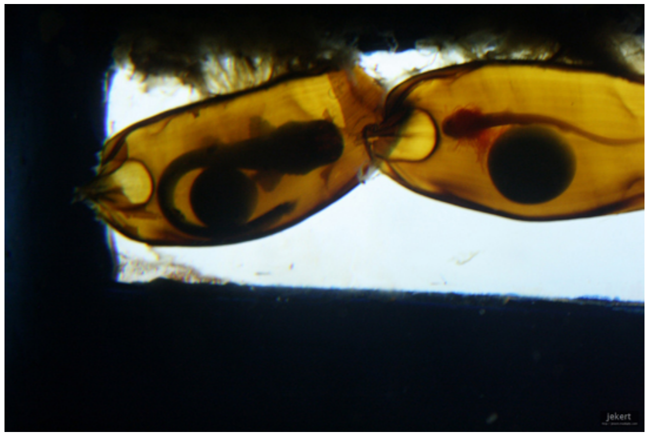

**Figure 29.14** Shark egg cases. Shark embryos are clearly visible through these transparent egg cases. The round structure is the yolk that nourishes the growing embryo. (credit: Jek Bacarisas)

In general, the Chondrichthyes have a fusiform or dorsoventrally flattened body, a *heterocercal* caudal fin or tail (unequally sized fin lobes, with the tail vertebrae extending into the larger upper lobe) paired pectoral and pelvic fins (in males these may be modified as claspers), exposed gill slits (*elasmobranch*), and an intestine with a spiral valve that condenses the length of the intestine. They also have three pairs of semicircular canals, and excellent senses of smell, vibration, vision, and electroreception. A very large lobed liver produces *squalene oil* (a lightweight biochemical precursor to steroids) that serves to aid in buoyancy (because with a specific gravity of 0.855, it is lighter than that of water).

Rays and skates comprise more than 500 species. They are closely related to sharks but can be distinguished from sharks by their flattened bodies, pectoral fins that are enlarged and fused to the head, and gill slits on their ventral surface (Figure 29.15). Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.

Unlike the stereotypical sharks and rays, the Holocephali (chimaeras or ratfish) have a *diphycercal* tail (equally sized fin lobes, with the tail vertebrae located between them), lack scales (lost secondarily in evolution), and have teeth modified as grinding plates that are used to feed on mollusks and other invertebrates (Figure 29.15b). Unlike sharks with elasmobranch or naked gills, chimaeras have four pairs of gills covered by an operculum. Many species have a pearly iridescence and are extremely pretty.

(a) (b)

**Figure 29.15** Cartilaginous fish. (a) Stingray. This stingray blends into the sandy bottom of the ocean floor. A spotted ratfish (b) Hydrolagus colliei credit a "Sailn1"/Flickr; (credit: a "Sailn1"/Flickr b: Linda Snook / MBNMS [Public domain], via Wikimedia Commons.)

## Osteichthyes: Bony Fishes

Members of the clade **Osteichthyes**, also called bony fishes, are characterized by a bony skeleton. The vast majority of present-day fishes belong to this group, which consists of approximately 30,000 species, making it the largest class of vertebrates in existence today.

Nearly all bony fishes have an *ossified skeleton* with specialized bone cells (osteocytes) that produce and maintain a calcium phosphate matrix. This characteristic has been reversed only in a few groups of Osteichthyes, such as sturgeons and paddlefish, which have primarily cartilaginous skeletons. The skin of bony fishes is often covered by overlapping scales, and glands in the skin secrete mucus that reduces drag when swimming and aids the fish in osmoregulation. Like sharks, bony fishes have a lateral line system that detects vibrations in water.

All bony fishes use gills to breathe. Water is drawn over gills that are located in chambers covered and ventilated by a protective, muscular flap called the operculum. Many bony fishes also have a **swim bladder**, a gas-filled organ derived as a pouch from the gut. The swim bladder helps to control the buoyancy of the fish. In most bony fish, the gases of the swim bladder are exchanged directly with the blood. The swim bladder is believed to be homologous to the lungs of lungfish and the lungs of land vertebrates.

Bony fishes are further divided into two extant clades: Class **Actinopterygii** (ray-finned fishes) and Class **Sarcopterygii** (lobe-finned fishes).

Actinopterygii (Figure 29.16a), the ray-finned fishes, include many familiar fishes—tuna, bass, trout, and salmon among others—and represent about half of all vertebrate species. Ray-finned fishes are named for the fan of slender bones that supports their fins.

In contrast, the fins of Sarcopterygii (Figure 29.16b) are fleshy and lobed, supported by bones that are similar in type and arrangement to the bones in the limbs of early tetrapods. The few extant members of this clade include several species of lungfishes and the less familiar coelacanths, which were thought to be extinct until living specimens were discovered between Africa and Madagascar. Currently, two species of coelocanths have been described.

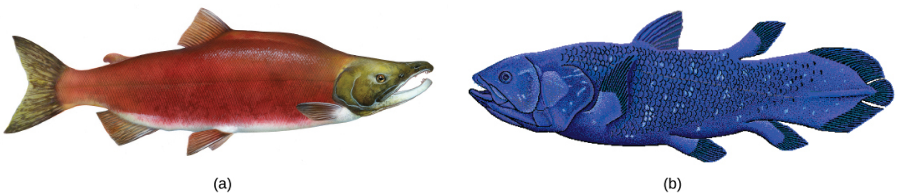


**Figure 29.16** Osteichthyes. The (a) sockeye salmon and (b) coelacanth are both bony fishes of the Osteichthyes clade. The coelacanth, sometimes called a lobe-finned fish, was thought to have gone extinct in the Late Cretaceous period, 100 million years ago, until one was discovered in 1938 near the Comoros Islands between Africa and Madagascar. (credit a: modification of work by Timothy Knepp, USFWS; credit b: modification of work by Robbie Cada)

# 29.3 Amphibians

*By the end of this section, you will be able to do the following:*

- Describe the important difference between the life cycle of amphibians and the life cycles of other vertebrates
- Distinguish between the characteristics of Urodela, Anura, and Apoda
- Describe the evolutionary history of amphibians

Amphibians are vertebrate tetrapods ("four limbs"), and include frogs, salamanders, and caecilians. The term "amphibian" loosely translates from the Greek as "dual life," which is a reference to the metamorphosis that many frogs and salamanders undergo and the unique mix of aquatic and terrestrial phases that are required in their life cycle. In fact, they cannot stray far from water because their reproduction is intimately tied to aqueous environments. Amphibians evolved during the Devonian period and were the earliest terrestrial tetrapods. They represent an evolutionary transition from water to land that occurred over many millions of years. Thus, the Amphibia are the only living true vertebrates that have made a transition from water to land in both their ontogeny (life development) and phylogeny (evolution). They have not changed much in morphology over the past 350 million years!

## LINK TO LEARNING

Watch this series of five Animal Planet videos on tetrapod evolution:

- 1: The evolution from fish to earliest tetrapod
  Click to view content (https://www.openstax.org/l/tetrapod_evol1)
- 2: Fish to Earliest Tetrapod
  Click to view content (https://www.openstax.org/l/tetrapod_evol2)
- 3: The discovery of coelacanth and *Acanthostega* fossils