CHAPTER 29
Vertebrates

Figure 29.1 Examples of critically endangered vertebrate species include (a) the Siberian tiger (*Panthera tigris*), (b) the mountain gorilla (*Gorilla beringei*), and (c) the harpy eagle (*Harpia harpyja*). (The harpy eagle is considered "near threatened" globally, but critically endangered in much of its former range in Mexico and Central America.) (credit a: modification of work by Dave Pape; credit b: modification of work by Dave Proffer; credit c: modification of work by Haui Ared)

INTRODUCTION Vertebrates are among the most recognizable organisms of the Animal Kingdom, and more than 62,000 vertebrate species have been identified. The vertebrate species now living represent only a small portion of the vertebrates that have existed in the past. The best-known extinct vertebrates are the dinosaurs, a unique group of reptiles, some of which reached sizes not seen before or after in *terrestrial* animals. In fact, they were the dominant terrestrial animals for 150 million years, until most of them died out in a mass extinction near the end of the Cretaceous period (except for the feathered theropod ancestors of modern birds, whose direct descendents now number nearly 10,000 species). Although it is not known with certainty what caused this mass extinction (not only of dinosaurs, but of many other groups of organisms), a great deal is known about the anatomy of the dinosaurs and early birds, given the preservation of numerous skeletal elements, nests, eggs, and embryos in the fossil record.

Chapter Outline

29.1 Chordates

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

- Describe the distinguishing characteristics of chordates
- Identify the derived characters of craniates that sets them apart from other chordates
- Describe the developmental fate of the notochord in vertebrates

The vertebrates exhibit two major innovations in their evolution from the invertebrate chordates. These innovations may be associated with the whole genome duplications that resulted in a quadruplication of the basic chordate genome, including the *Hox* gene loci that regulate the placement of structures along the three axes of the body. One of the first major steps was the emergence of the quadrupeds in the form of the amphibians. A second step was the evolution of the amniotic egg, which, similar to the evolution of pollen and seeds in plants, freed terrestrial animals from their dependence on water for fertilization and embryonic development. Within the amniotes, modifications of keratinous epidermal structures have given rise to scales, claws, hair, and feathers. The scales of reptiles sealed their skins against water loss, while hair and feathers provided insulation to support the evolution of endothermy, as well as served other functions such as camouflage and mate attraction in the vertebrate lineages that led to birds and mammals.

Currently, a number of vertebrate species face extinction primarily due to habitat loss and pollution. According to the International Union for the Conservation of Nature, more than 6,000 vertebrate species are classified as threatened. Amphibians and mammals are the classes with the greatest percentage of threatened species, with 29 percent of all amphibians and 21 percent of all mammals classified as threatened. Attempts are being made around the world to prevent the extinction of threatened species. For example, the Biodiversity Action Plan is an international program, ratified by 188 countries, which is designed to protect species and habitats.

Vertebrates are members of the kingdom Animalia and the phylum Chordata (Figure 29.2). Recall that animals that possess bilateral symmetry can be divided into two groups—protostomes and deuterostomes—based on their patterns of embryonic development. The deuterostomes, whose name translates as "second mouth," consist of two major phyla: Echinodermata and Chordata. Echinoderms are invertebrate marine animals that have pentaradial symmetry and a spiny body covering, a group that includes sea stars, sea urchins, and sea cucumbers. The most conspicuous and familiar members of Chordata are vertebrates, but this phylum also includes two groups of invertebrate chordates.

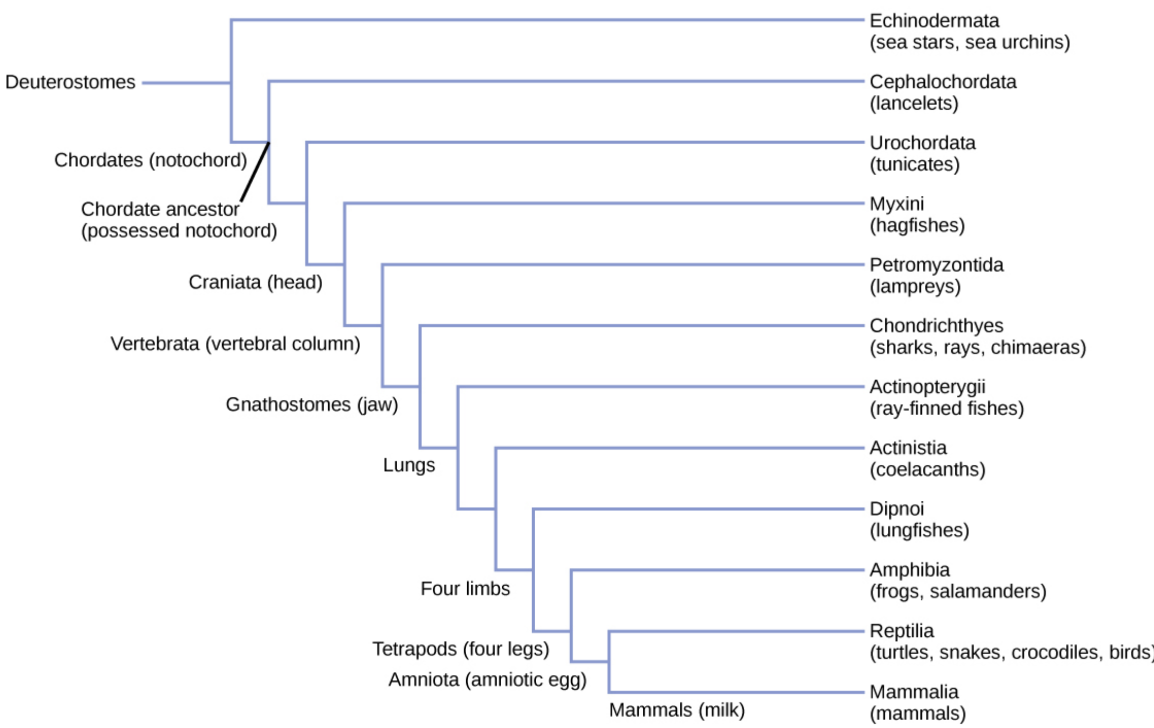

Figure 29.2 Deuterostome phylogeny. All chordates are deuterostomes possessing a notochord at some stage of their life cycle.

Characteristics of Chordata

Animals in the phylum **Chordata** share five key chacteristics that appear at some stage during their development: a notochord, a dorsal hollow (tubular) nerve cord, pharyngeal gill arches or slits, a post-anal tail, and an endostyle/thyroid gland (Figure 29.3). In some groups, some of these key chacteristics are present only during embryonic development.

The chordates are named for the **notochord**, which is a flexible, rod-shaped mesodermal structure that is found in the embryonic stage of all chordates and in the adult stage of some chordate species. It is strengthened with glycoproteins similar to cartilage and covered with a collagenous sheath. The notocord is located between the digestive tube and the nerve cord, and provides rigid skeletal support as well as a flexible location for attachment of axial muscles. In some chordates, the notochord acts as the primary axial support of the body throughout the animal's lifetime. However, in vertebrates (craniates), the notochord is present only during embryonic development, at which time it induces the development of the neural tube and serves as a support for the developing embryonic body. The notochord, however, is not found in the postembryonic stages of vertebrates; at this point, it has been replaced by the vertebral column (that is, the spine).

VISUAL CONNECTION

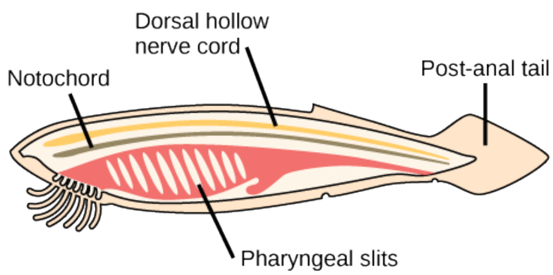

Figure 29.3 Chordate features. In chordates, four common features appear at some point during development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. The endostyle is embedded in the floor of the pharynx.

Which of the following statements about common features of chordates is true?

1. The dorsal hollow nerve cord is part of the chordate central nervous system.
2. In vertebrate fishes, the pharyngeal slits become the gills.
3. Humans are not chordates because humans do not have a tail.
4. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.
5. The endostyle secretes steroid hormones.

The **dorsal hollow nerve cord** is derived from ectoderm that rolls into a hollow tube during development. In chordates, it is located dorsally to the notochord. In contrast, the nervous system in protostome animal phyla is characterized by solid nerve cords that are located either ventrally and/or laterally to the gut. In vertebrates, the neural tube develops into the brain and spinal cord, which together comprise the central nervous system (CNS). The peripheral nervous system (PNS) refers to the peripheral nerves (including the cranial nerves) lying outside of the brain and spinal cord.

Pharyngeal slits are openings in the pharynx (the region just posterior to the mouth) that extend to the outside environment. In organisms that live in aquatic environments, pharyngeal slits allow for the exit of water that enters the mouth during feeding. Some invertebrate chordates use the pharyngeal slits to filter food out of the water that enters the mouth. The endostyle is a strip of ciliated mucus-producing tissue in the floor of the pharynx. Food particles trapped in the mucus are moved along the endostyle toward the gut. The endostyle also produces substances similar to thyroid hormones and is homologous with the thyroid gland in vertebrates. In vertebrate fishes, the pharyngeal slits are modified into gill supports, and in jawed fishes, into jaw supports. In tetrapods (land vertebrates), the slits are highly modified into components of the ear, and tonsils and thymus glands. In other vertebrates, pharyngeal arches, derived from all three germ layers, give rise to the oral jaw from the first pharyngeal arch, with the second arch becoming the hyoid and jaw support.

The **post-anal tail** is a posterior elongation of the body, extending beyond the anus. The tail contains skeletal elements and muscles, which provide a source of locomotion in aquatic species, such as fishes. In some terrestrial vertebrates, the tail also helps with balance, courting, and signaling when danger is near. In humans and other great apes, the post-anal tail is reduced to a vestigial coccyx ("tail bone") that aids in balance during sitting.

LINK TO LEARNING

Click for a video discussing the evolution of chordates and five characteristics that they share.

[Click to view content (https://www.openstax.org/l/chordate_evol)](https://www.openstax.org/l/chordate_evol)

Chordates and the Evolution of Vertebrates

Two clades of chordates are invertebrates: Cephalochordata and Urochordata. Members of these groups also possess the five distinctive features of chordates at some point during their development.

Cephalochordata

Members of **Cephalochordata** possess a notochord, dorsal hollow tubular nerve cord, pharyngeal slits, endostyle/thyroid gland, and a post-anal tail in the adult stage (Figure 29.4). The notochord extends into the head, which gives the subphylum its name. Although the neural tube also extends into the head region, there is no well-defined brain, and the nervous system is centered around a hollow nerve cord lying above the notochord. Extinct members of this subphylum include *Pikaia*, which is the oldest known cephalochordate. Excellently preserved *Pikaia* fossils were recovered from the Burgess shales of Canada and date to the middle of the Cambrian age, making them more than 500 million years old. Its anatomy of *Pikaia* closely resembles that of the extant lancelet in the genus *Branchiostoma*.

The lancelets are named for their bladelike shape. Lancelets are only a few centimeters long and are usually found buried in sand at the bottom of warm temperate and tropical seas. Cephalochordates are suspension feeders. A water current is created by cilia in the mouth, and is filtered through oral tentacles. Water from the mouth then enters the pharyngeal slits, which filter out food particles. The filtered water collects in a gill chamber called the **atrium** and exits through the **atriopore**. Trapped food particles are caught in a stream of mucus produced by the endostyle in a ventral ciliated fold (or groove) of the pharynx and carried to the gut. Most gas exchange occurs across the body surface. Sexes are separate and gametes are released into the water through the atriopore for external fertilization.

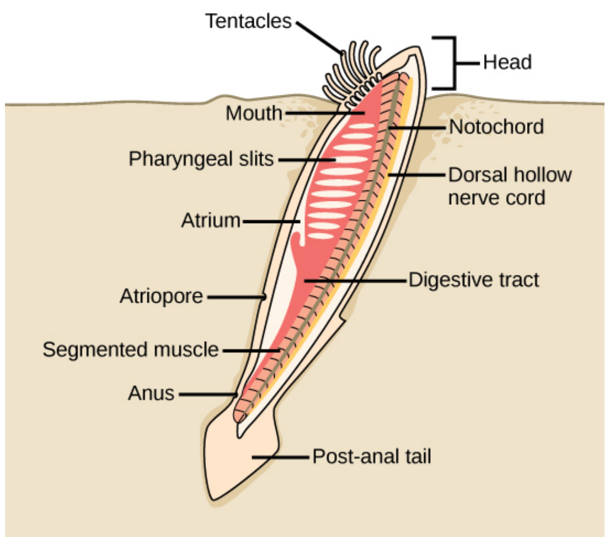

Figure 29.4 Cephalochordate anatomy. In the lancelet and other cephalochordates, the notochord extends into the head region. Adult lancelets retain all five key characteristics of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, an endostyle, and a post-anal tail.

Urochordata

The 1,600 species of **Urochordata** are also known as **tunicates** (Figure 29.5). The name tunicate derives from the cellulose-like carbohydrate material, called the **tunic**, which covers the outer body of tunicates. Although tunicates are classified as chordates, the adults do *not* have a notochord, a dorsal hollow nerve cord, or a post-anal tail, although they do have pharyngeal slits and an endostyle. The "tadpole" larval form, however, possesses all five structures. Most tunicates are hermaphrodites; their larvae hatch from eggs inside the adult tunicate's body. After hatching, a tunicate larva (possessing all five chordate features) swims for a few days until it finds a suitable surface on which it can attach, usually in a dark or shaded location. It then attaches via the head to the surface and undergoes metamorphosis into the adult form, at which point the notochord, nerve cord, and tail disappear, leaving the pharyngeal gill slits and the endostyle as the two remaining features of its chordate morphology.

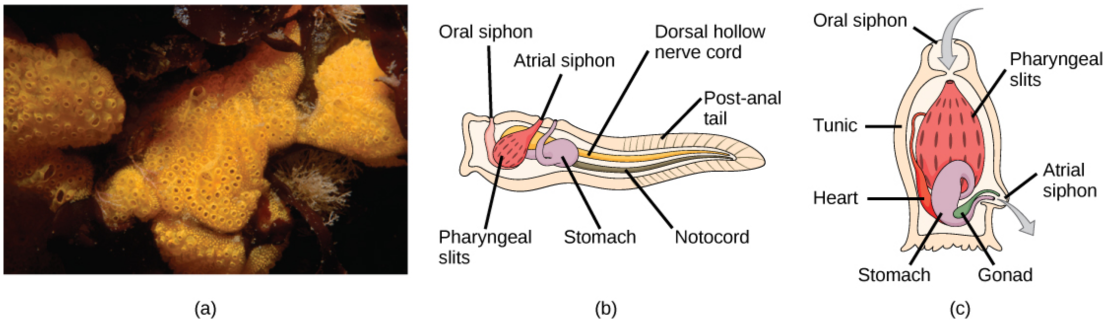

Figure 29.5 Urochordate anatomy. (a) This photograph shows a colony of the tunicate *Botrylloides violaceus*. (b) The larval stage of the tunicate possesses all of the features characteristic of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, an endostyle, and a post-anal tail. (c) In the adult stage, the notochord, nerve cord, and tail disappear, leaving just the pharyngeal slits and endostyle. (credit: modification of work by Dann Blackwood, USGS)

Adult tunicates may be either solitary or colonial forms, and some species may reproduce by budding. Most tunicates live a sessile existence on the ocean floor and are *suspension feeders*. However, chains of thaliacean tunicates called *salps* (Figure 29.6) can swim actively while feeding, propelling themselves as they move water through the pharyngeal slits. The primary foods of tunicates are plankton and detritus. Seawater enters the tunicate's body through its incurrent siphon. Suspended material is filtered out of this water by a mucous net produced by the endostyle and is passed into the intestine via the action of cilia. The anus empties into the excurrent siphon, which expels wastes and water. Tunicates are found in shallow ocean waters around the world.

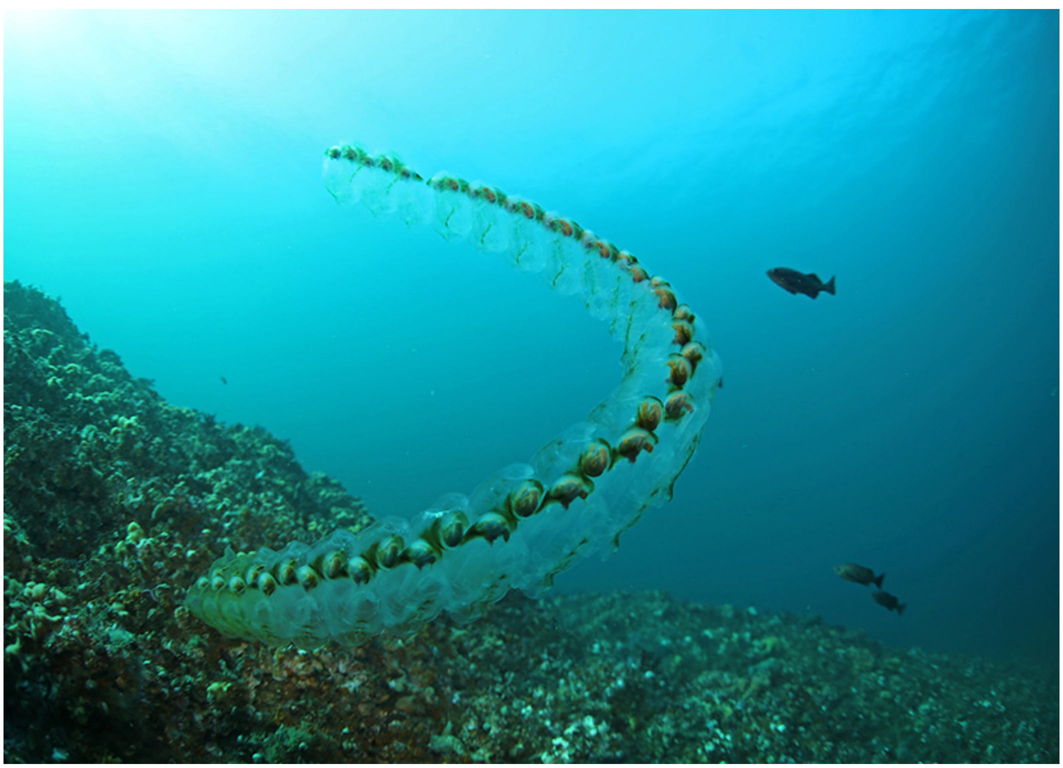

Figure 29.6 Salps. These colonial tunicates feed on phytoplankton. Salps are sequential hermaphrodites, with younger female colonies fertilized by older male colonies. (credit: Oregon Department of Fish & Wildlife via Wikimedia Commons)

Subphylum Vertebrata (Craniata)

A **cranium** is a bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones (Figure 29.7). Most bilaterally symmetrical animals have a head; of these, those that have a cranium comprise the clade Craniata/Vertebrata, which includes the primitively jawless Myxini (hagfishes), Petromyzontida (lampreys), and all of the organisms called "vertebrates." (We should note that the Myxini have a cranium but lack a backbone.)

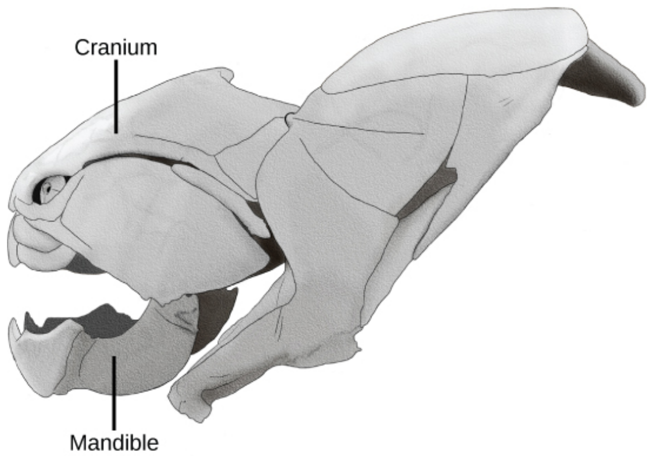

Figure 29.7 A craniate skull. The subphylum **Craniata (or Vertebrata)**, including this placoderm fish (*Dunkleosteus* sp.), are characterized by the presence of a cranium, mandible, and other facial bones. (credit: "Steveoc 86"/Wikimedia Commons)

Members of the phylum Craniata/Vertebrata display the five characteristic features of the chordates; however, members of this group also share derived characteristics that distinguish them from invertebrate chordates. Vertebrates are named for the vertebral column, composed of **vertebrae**—a series of separate, irregularly shaped bones joined together to form a backbone (Figure 29.8). Initially, the vertebrae form in segments around the embryonic notochord, but eventually replace it in adults. In most derived vertebrates, the notochord becomes the *nucleus pulposus* of the intervertebral discs that cushion and support adjacent vertebrae.

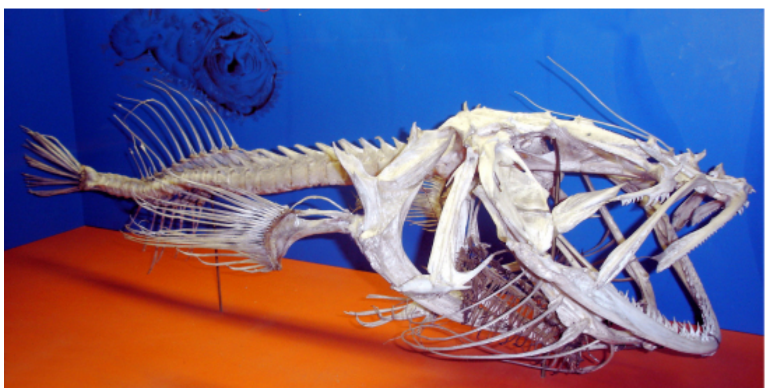

Figure 29.8 A vertebrate skeleton. Vertebrata are characterized by the presence of a backbone, such as the one that runs through the middle of this fish. All vertebrates are in the Craniata clade and have a cranium. (credit: Ernest V. More; taken at Smithsonian Museum of Natural History, Washington, D.C.)

The relationship of the vertebrates to the invertebrate chordates has been a matter of contention, but although these cladistic relationships are still being examined, it appears that the Craniata/Vertebrata are a monophyletic group that shares the five basic chordate characteristics with the other two subphyla, Urochordata and Cephalochordata. Traditional phylogenies place the cephalochordates as a sister clade to the chordates, a view that has been supported by most current molecular analyses. This hypothesis is further supported by the discovery of a fossil in China from the genus *Haikouella*. This organism seems to be an intermediate form between cephalochordates and vertebrates. The *Haikouella* fossils are about 530 million years old and appear similar to modern lancelets. These organisms had a brain and eyes, as do vertebrates, but lack the skull found in craniates.[1] This evidence suggests that vertebrates arose during the Cambrian explosion.

Vertebrates are the largest group of chordates, with more than 62,000 living species, which are grouped based on anatomical and physiological traits. More than one classification and naming scheme is used for these animals. Here we will consider the *traditional groups* Agnatha, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia, which constitute classes in the subphylum Vertebrata/Craniata. Virtually all modern cladists classify birds within Reptilia, which correctly reflects their

1Chen, J. Y., Huang, D. Y., and Li, C. W., "An early Cambrian craniate-like chordate," *Nature* 402 (1999): 518–522, doi:10.1038/990080.

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!