Deuterostome Animals

34

In most habitats the "top predators"—meaning animals that prey on other animals and aren't preyed upon themselves—are deuterostomes.

KEY CONCEPTS

- The most species-rich deuterostome lineages are the echinoderms and the vertebrate groups called ray-finned fishes and tetrapods.
- Echinoderms and vertebrates have unique body plans. Echinoderms are radially symmetric as adults and have a water vascular system. All vertebrates have a skull and an extensive endoskeleton made of cartilage or bone.
- The diversification of echinoderms was triggered by the evolution of appendages called podia; the diversification of vertebrates was driven by the evolution of the jaw and limbs.
- Humans are a tiny twig on the tree of life. Chimpanzees and humans diverged from a common ancestor that lived in Africa 6–7 million years ago. Since then, at least 14 humanlike species have existed.

The **deuterostomes** include the largest-bodied and some of the most morphologically complex of all animals. They range from the sea stars that cling to dock pilings, to the fish that dart in and out of coral reefs, to the wildebeests that migrate across the Serengeti Plains of East Africa.

Biologists are drawn to deuterostomes in part because of their importance in the natural and human economies. Deuterostomes may not be as numerous as insects and other protostomes, but they act as key predators and herbivores in most marine and terrestrial habitats. If you diagram a food chain that traces the flow of energy from algae or plants up through several levels of consumers (see Chapter 30), deuterostomes are almost always at the top of the chain. In addition, humans rely on deuterostomes—particularly **vertebrates**, or animals with backbones—for food and power. Fish and domesticated livestock are key sources of protein in most cultures, and in the developing world agriculture is still based on the power generated by oxen, horses, water buffalo, or mules. In industrialized countries, millions of people bird-watch, plan vacations around seeing large mammals in national parks, or keep vertebrates as pets. Humans are deuterostomes—we have a special interest in our closest relatives, and a special fondness for them.

To introduce this key group, let's begin with an overview of the morphological traits that distinguish major lineages of deuterostomes and then delve into the phylogenetic relationships among the major vertebrate groups and the evolutionary innovations that led to their diversification. After summarizing the key characteristics of deuterostome lineages, the chapter closes with an introduction to human evolution.

Key Concept | Important Information | Practise It

34.1 An Overview of Deuterostome Evolution

Most biologists recognize just four phyla of deuterostomes: the Echinodermata, the Hemichordata, the Xenoturbellida, and the Chordata (**Figure 34.1**). The echinoderms include the sea stars and sea urchins. The hemichordates, or "acorn worms," are probably unfamiliar to you—they burrow in marine sands or muds and make their living by deposit feeding or suspension feeding. A lone genus with two wormlike species, called *Xenoturbella,* was recognized as a distinct phylum in 2006. The chordates include the vertebrates. The vertebrates, in turn, comprise the sharks, bony fishes, amphibians, reptiles (including birds), and mammals. Animals that are not vertebrates are collectively known as **invertebrates**. Echinoderms, hemichordates, and *Xenoturbella* are considered invertebrates, even though they are deuterostomes.

The deuterostomes were initially grouped together because they all undergo early embryonic development in a similar way. When a humpback whale, sea urchin, or human is just beginning to grow, cleavage is radial, the gut starts developing from posterior to anterior—with the anus forming first and the mouth second—and a coelom (if present) develops from outpocketings of mesoderm (see Chapter 32).

Although deuterostomes share important features of embryonic development, their adult body plans and their feeding methods, modes of locomotion, and means for reproduction are highly diverse. Let's explore who the deuterostome animals are and how they diversified, starting with the morphological traits that distinguish the echinoderms, chordates, and vertebrates.

What Is an Echinoderm?

All deuterostomes are considered bilaterians because they evolved from an ancestor that was bilaterally symmetric (see Chapter 32). But a remarkable event occurred early in the evolution of echinoderms: The origin of a unique type of type of radial symmetry. Adult **echinoderms** have bodies with five-sided radial symmetry, called pentaradial symmetry (**Figure 34.2a**), even though both their larvae and their ancestors are bilaterally symmetric (**Figure 34.2b**).

Recall from Chapter 32 that radially symmetric animals do not have well-developed head and posterior regions. As a result, they tend to interact with the environment in all directions at once instead of facing the environment in one direction. If adult echinoderms are capable of movement, they tend to move equally well in all directions instead of only headfirst.

The other remarkable event in echinoderm evolution was the origin of a unique morphological feature: a series of branching, fluid-filled tubes and chambers called the **water vascular system** (**Figure 34.3a**). One of the tubes is open to the exterior where it meets the body wall, so seawater can flow into and out of the system. Inside, fluids move via the beating of cilia that line the interior of the tubes and chambers. In effect, the water vascular system forms a sophisticated hydrostatic skeleton.

Figure 34.3a highlights a particularly important part of the system called tube feet. **Tube feet** are elongated, fluid-filled structures. **Podia** (literally, "feet") are sections of the tube feet that project outside the body (**Figure 34.3b**) and make contact with the substrate. As podia extend and contract in a coordinated way along the base of an echinoderm, they alternately grab and release the substrate. As a result, the individual moves.

The other noteworthy feature of the echinoderm body is its **endoskeleton**, which is a hard, supportive structure located just inside a thin layer of epidermal tissue. (The structure in Figure 34.2a is an endoskeleton.) As an individual is developing, cells secrete plates of calcium carbonate inside the skin. Depending on the species involved, the plates may remain independent and result in a flexible structure or fuse into a rigid

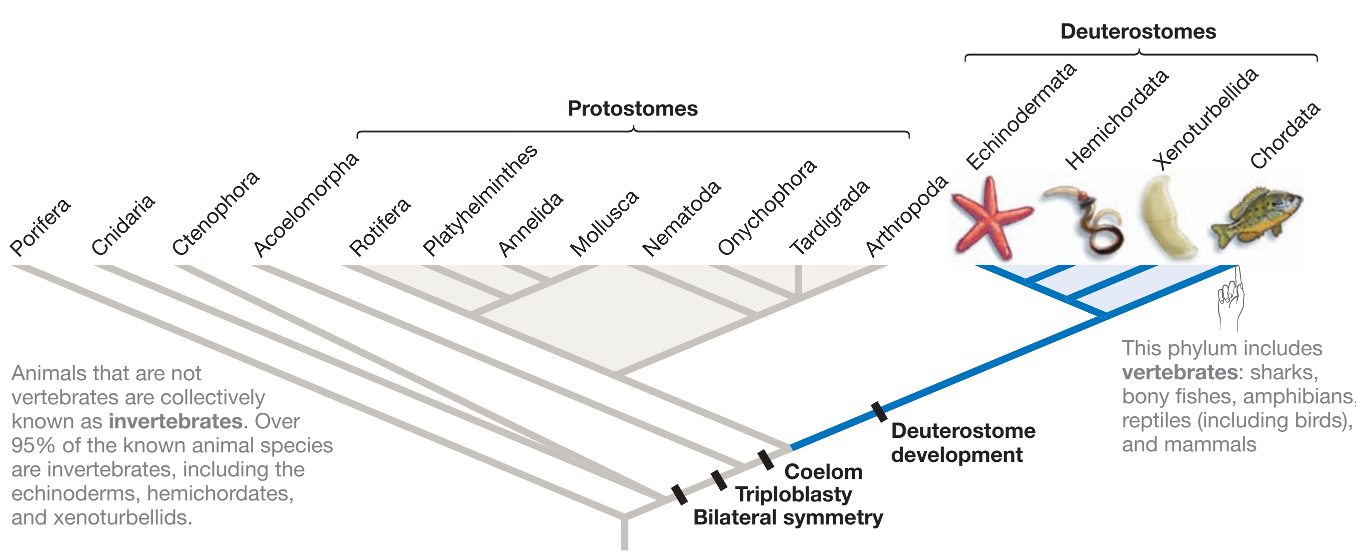


FIGURE 34.1 There Are Four Phyla of Deuterostomes. The deuterostomes comprise the phyla Echinodermata, Hemichordata, Xenoturbellida, and Chordata. The vertebrates are a subphylum of chordates.

QUESTION Are invertebrates a monophyletic or a paraphyletic group?

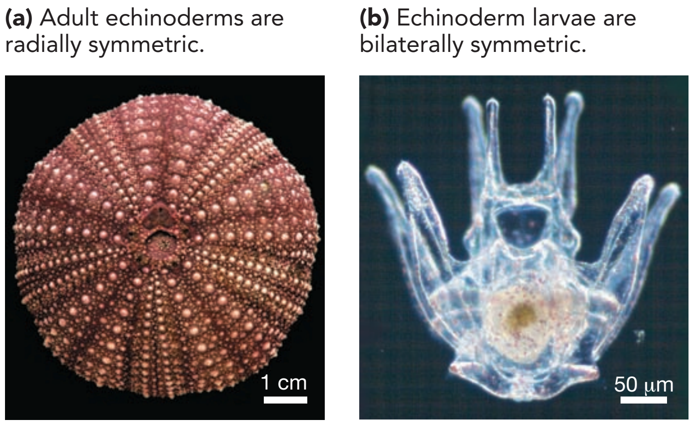


FIGURE 34.2 Body Symmetry Differs in Adult and Larval Echinoderms. **(a)** The skeleton of an adult and **(b)** the larva of sea urchin *Strongylocentrotus franciscanus*. Bilaterally symmetric larvae undergo metamorphosis and emerge as radially symmetric adults.

QUESTION Why are echinoderms considered members of the lineage called Bilateria (bilaterally symmetric animals)?

case. Along with radial symmetry and the water vascular system, this type of endoskeleton is a synapomorphy—a trait that identifies echinoderms as a monophyletic group. If you understand this concept, you should be able to indicate the origin of pentaradial symmetry in adults, the water vascular system, and the echinoderm endoskeleton on Figure 34.1.

Two other phyla form a monophyletic group with echinoderms: Xenoturbellida and Hemichordata. The xenoturbellids ("strange-flatworms") have extremely simple, wormlike body plans. They don't have a gut, coelom, or brain, and they make their living absorbing nutrients in aquatic sediments. The hemichordates got their "half-chordates" name because they have an unusual feature found in chordates—openings into the throat called **pharyngeal gill slits**. The hemichordates are suspension feeders that live buried in muddy habitats on the ocean floor. As **Figure 34.4** shows, their pharyngeal gill slits function in feeding and gas exchange. Water enters the mouth, flows through structures where oxygen and food particles are extracted, and exits through the pharyngeal gill slits. They are not members of the phylum Chordata, however, because they lack several defining features shared by chordates. If you understand this point, you should be able to indicate two events on Figure 34.1: the origin of the pharyngeal gill slits observed in hemichordates and chordates, and the loss of pharyngeal gill slits in echinoderms and *Xenoturbella*.

What Is a Chordate?

The **chordates** are defined by the presence of four morphological features: (1) pharyngeal gill slits; (2) a stiff and supportive but flexible rod called a **notochord**, which runs the length of the body; (3) a bundle of nerve cells that runs the length of the body and forms a dorsal hollow **nerve cord**; and (4) a muscular, post-anal tail—meaning a tail that contains muscle and extends past the anus.

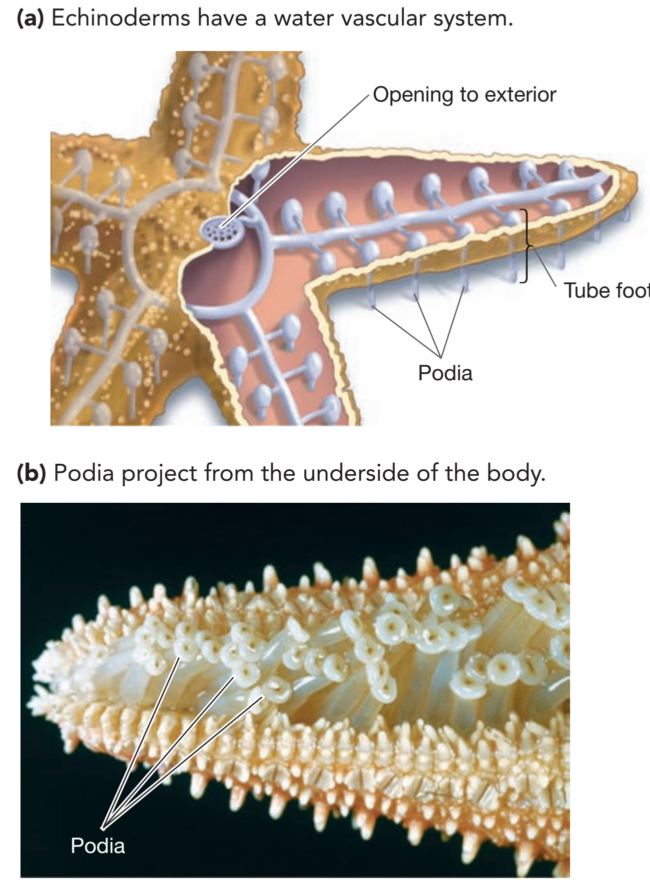


FIGURE 34.3 Echinoderms Have a Water Vascular System. (a) The water vascular system is a series of tubes and reservoirs that radiates throughout the body, forming a sophisticated hydrostatic skeleton. **(b)** Podia aid in movement because they extend from the body and can grab and release the substrate.

EXERCISE Echinoderms have an endoskeleton just under their skin, which functions in protection. Label it in part (a).

The phylum Chordata is made up of three major lineages, traditionally called subphyla: the (1) urochordates, (2) cephalochordates, and (3) vertebrates. All four defining characteristics of chordates—pharyngeal gill slits, notochords, dorsal hollow nerve cords, and tails—are found in these species.

- **Urochordates** are also called tunicates. As **Figure 34.5a** shows, pharyngeal gill slits are present in both larvae and adults and function in both feeding and gas exchange, much

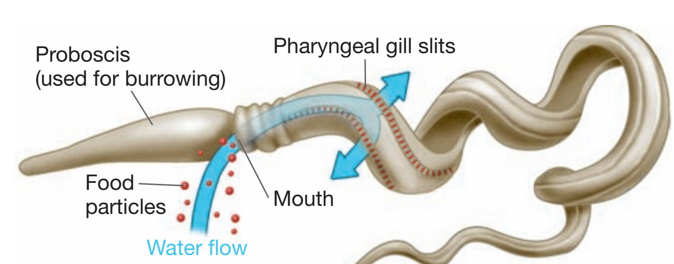


FIGURE 34.4 Hemichordates Suspension Feed Via Pharyngeal Gill Slits. The hemichordates, also known as acorn worms, burrow in marine muds and suspension feed as shown.

as they do in hemichordates. The notochord, dorsal hollow nerve cord, and tail are present only in the larvae, however. Because the notochord stiffens the tail, muscular contractions on either side of a larva's tail wag it back and forth and result in swimming movements. As larvae swim or float in the upper water layers of the ocean, they drift to new habitats where food might be more abundant.

Urochordates underline one of the most fundamental conclusions about chordate evolution: The four features that distinguish the group enabled new types of feeding and movement. Pharyngeal gill slits function in suspension feeding in the adult. The notochord functions as a simple endoskeleton in the larva, while nerves organized into the dorsal cord stimulate muscles in the tail that make efficient swimming movements possible.

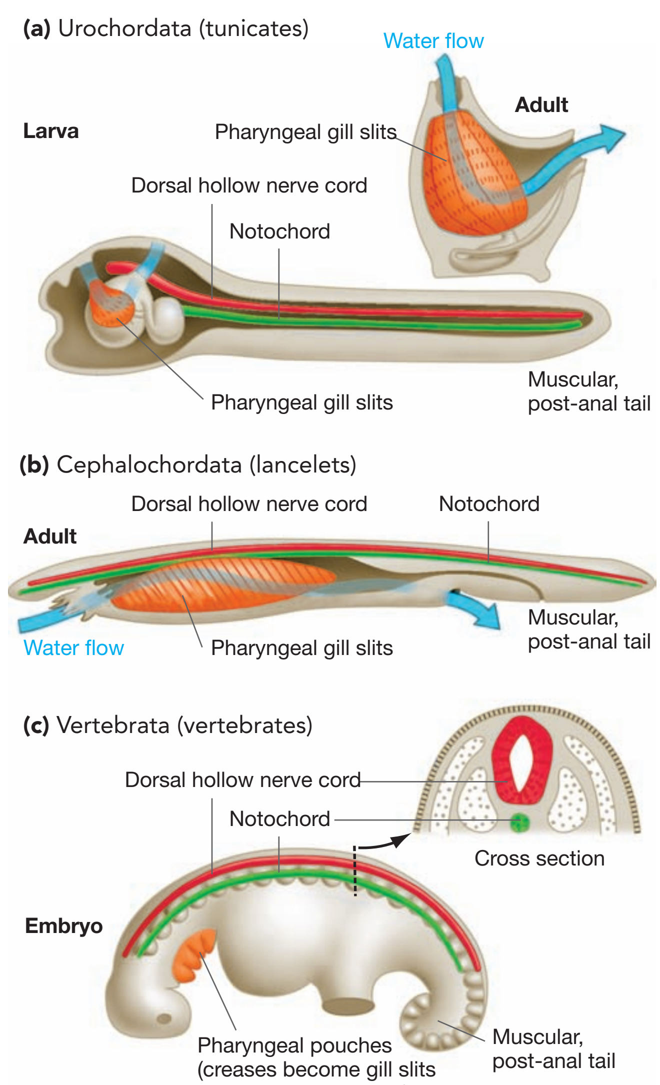


FIGURE 34.5 Four Traits Distinguish the Chordates. In chordates, either larvae or adults or both have notochords and muscular tails in addition to pharyngeal gill slits and dorsal hollow nerve cords. The three major chordate lineages are (a) tunicates, (b) lancelets, and (c) vertebrates.

QUESTION In tunicate larvae and in lancelets, what is the function of the notochord and tail?

- **Cephalochordates** are also called lancelets or amphioxus; they are small, mobile suspension feeders that look a little like fish (**Figure 34.5b**). Adult cephalochordates live in ocean-bottom habitats, where they burrow in sand and suspension feed with the aid of their pharyngeal gill slits. The cephalochordates also have a notochord that stiffens their bodies, so that muscle contractions on either side result in fishlike movement when they swim during dispersal or mating.
- Vertebrates (**Figure 34.5c**) include the sharks, several lineages of fishes (see **Box 34.1**), amphibians, reptiles (including birds), and mammals. In vertebrates, the dorsal hollow nerve cord is elaborated into the familiar spinal cord—a bundle of nerve cells that runs from the brain to the posterior of the body. Structures called pharyngeal pouches are present in all vertebrate embryos. In aquatic species, the creases between pouches open into gill slits and develop into part of the main gas-exchange organ—the **gills**. In terrestrial species, however, gill slits do not develop after the pharyngeal pouches form. A notochord also appears in all vertebrate embryos. Instead of functioning in body support and movement, though, it helps organize the body plan. You might recall from Chapter 22 that cells in the notochord secrete proteins that help induce the formation of **somites**, which are segmented blocks of tissue that form along the length of the body. Although the notochord itself disappears, cells in the somites later differentiate into the vertebrae, ribs, and skeletal muscles of the back, body wall, and limbs. In this way, the notochord is instrumental in the development of the trait that gave vertebrates their name.

What Is a Vertebrate?

The vertebrates are a monophyletic group distinguished by two traits: a column of cartilaginous or bony structures, called **vertebrae**, that form along the dorsal sides of most species, and a **cranium**, or skull—a bony, cartilaginous, or fibrous case that encloses the brain. The vertebral column is important because it protects the spinal cord. The cranium is important because it protects the brain along with sensory organs such as eyes.

The vertebrate brain develops as an outgrowth of the most anterior end of the dorsal hollow nerve cord and is important to the vertebrate lifestyle. Vertebrates are active predators and herbivores that can make rapid, directed movements with the aid of their endoskeleton. Coordinated movements are possible in part because vertebrates have large brains divided into three distinct regions: (1) a **forebrain**, housing the sense of smell; (2) a **midbrain**, associated with vision; and (3) a **hindbrain**, responsible for balance and hearing. In vertebrate groups that evolved more recently, the forebrain is a large structure called the **cerebrum**, and the hindbrain consists of enlarged regions called the **cerebellum** and **medulla oblongata**. (The structure and functions of the vertebrate brain are analyzed in detail in

BOX 34.1 What Is a Fish?

In everyday English, people use the word *fish* to mean just about any vertebrate that lives in water and has a streamlined body and fins. But to a biologist, saying that an organism is a fish prompts a question: Which fish?

As the blue branches on Figure 34.7 show, there is no monophyletic group that includes all of the fishlike lineages. Instead, "fishy" organisms are a series of independent monophyletic groups. Taken together, they form what biologists call a **grade**—a sequence of lineages that are paraphyletic. You might recall from Chapter 30 that the seedless vascular plants also form a grade and are paraphyletic.

In naming schemes that recognize only monophyletic groups, there is no such thing as a fish. Instead, there are jawless fishes, cartilaginous fishes (sharks and rays), lobe-finned fishes, lungfishes, and ray-finned fishes. Each of the monophyletic fish groups will be explored in more detail in Section 34.5. If you understand the difference between a paraphyletic and monophyletic group, you should be able to draw what Figure 34.7 would look like if there actually were a monophyletic group called "The Fish."

Chapter 45.) The evolution of a large brain, protected by a hard cranium, was a key innovation in vertebrate evolution.

Check Your Understanding

If you understand that...

- The deuterostomes include four phyla: the echinoderms, hemichordates, xenoturbellids, and chordates.
- Within the chordates, the vertebrates are the most species-rich and morphologically diverse subphylum.

You should be able to...

1) Draw a simple phylogenetic tree showing the relationships among the echinoderm, hemichordate, chordate, and vertebrate lineages.
2) Identify the key innovations that distinguish each of these four groups.
3) Explain why each of these innovations is important in feeding or movement.

34.2 An Overview of Vertebrate Evolution

Vertebrates have been the focus of intense research for well over 300 years, in part because they are large and conspicuous and in part because they include the humans. All this effort has paid off in an increasingly thorough understanding of how the vertebrates diversified. Let's consider what data from the fossil record have to say about key events in vertebrate evolution, then examine the current best estimate of the phylogenetic relationships among vertebrates.

The Vertebrate Fossil Record

Both echinoderms and vertebrates are present in the Burgess Shale deposits that formed during the Cambrian explosion 542–488 million years ago (see also Chapter 27). The vertebrate fossils in these rocks show that the earliest members of this lineage lived in the ocean about 540 million years ago, had streamlined, fishlike bodies, and appear to have had a skull made of cartilage. **Cartilage** is a stiff tissue that consists of scattered cells in a gel-like matrix of polysaccharides and protein fibres. Several groups of early vertebrates had endoskeletons made of cartilage, as do the sharks and rays living today.

Following the appearance of vertebrates, the fossil record documents a series of key innovations that occurred as this lineage diversified (**Figure 34.6**):

- Fossil vertebrates from the early part of the Silurian period, about 440 million years ago, are the first fossils to have bone. **Bone** is a tissue consisting of cells and blood vessels encased in a matrix made primarily of a calcium- and phosphate-containing compound called hydroxyapatite, along with a small amount of protein fibres. When bone first evolved, it did not occur in the endoskeleton. Instead, bone was deposited in scalelike plates that formed an **exoskeleton**—a hard, hollow structure that envelops the body. Based on the fossils' overall morphology, biologists infer that these animals swam with the aid of a notochord and that they breathed and fed by gulping water and filtering it through their pharyngeal gill slits. Presumably, the bony plates helped provide protection from predators.
- The first bony fish with jaws show up in the fossil record about 400 million years ago. The evolution of jaws was significant because it gave vertebrates the ability to bite, meaning that they were no longer limited to suspension feeding or deposit feeding. Instead, they could make a living as herbivores or predators. Soon after, jawbones with teeth appear in the fossil record. With jaws and teeth, vertebrates became armed and dangerous. The fossil record shows that a spectacular radiation of jawed fishes followed, filling marine and freshwater habitats.
- The next great event in the evolution of vertebrates was the transition to living on land. The first animals that had limbs and were capable of moving on land are dated to about 365 million years ago. These were the first of the **tetrapods** ("four-footed")—animals with four limbs (Figure 34.6).

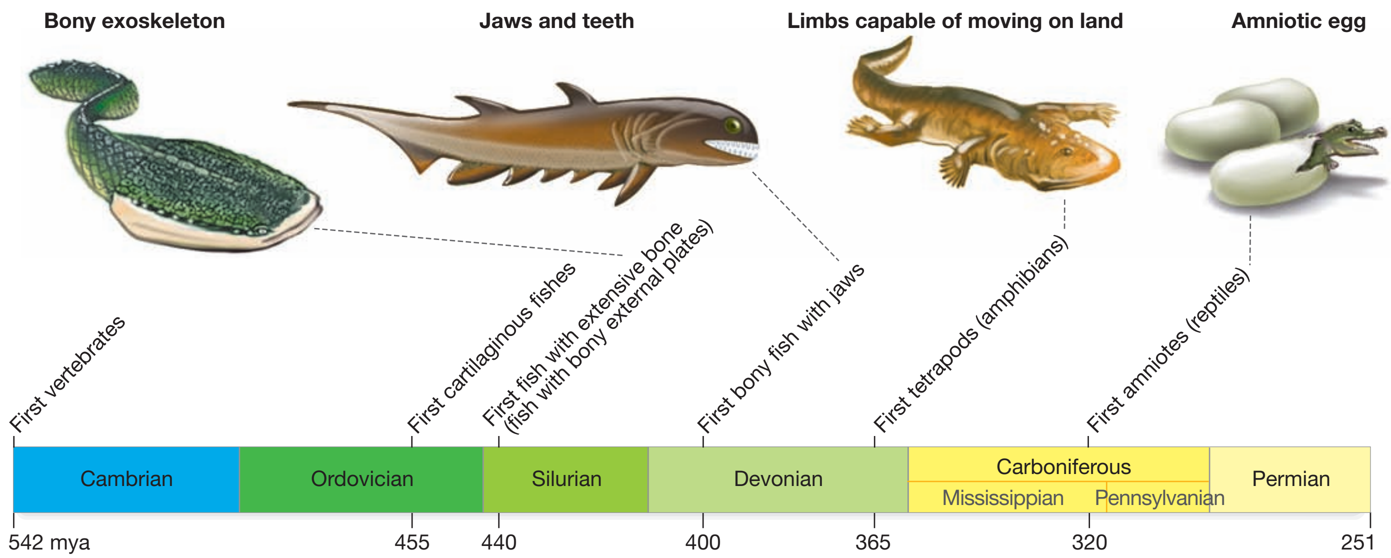


FIGURE 34.6 Timeline of the Vertebrate Fossil Record.

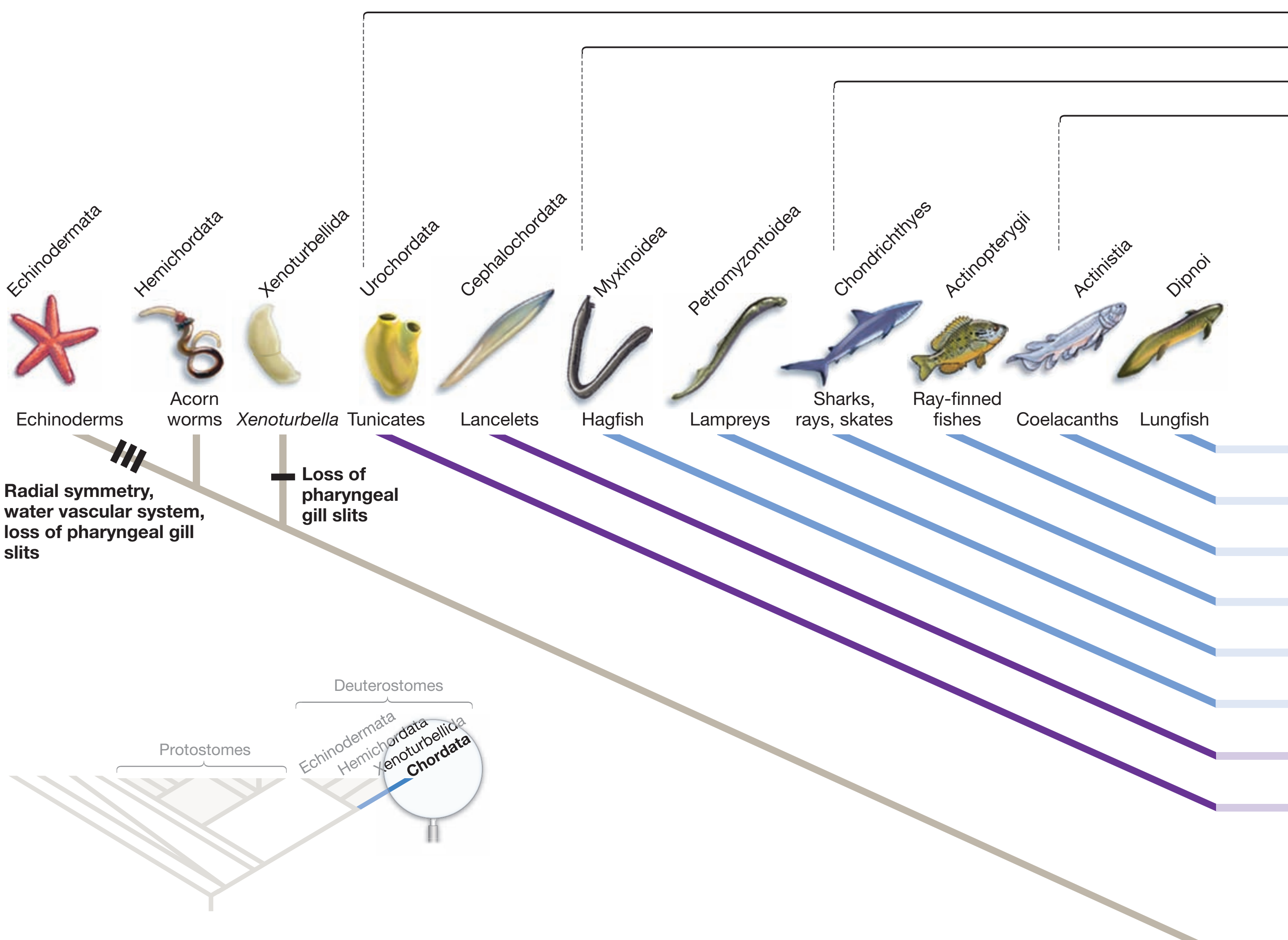


FIGURE 34.7 A Phylogeny of the Chordates. A chordate phylogeny showing the relationships among the major groups within the subphylum vertebrata. The short bars indicate where major innovations occurred as the lineages diversified.

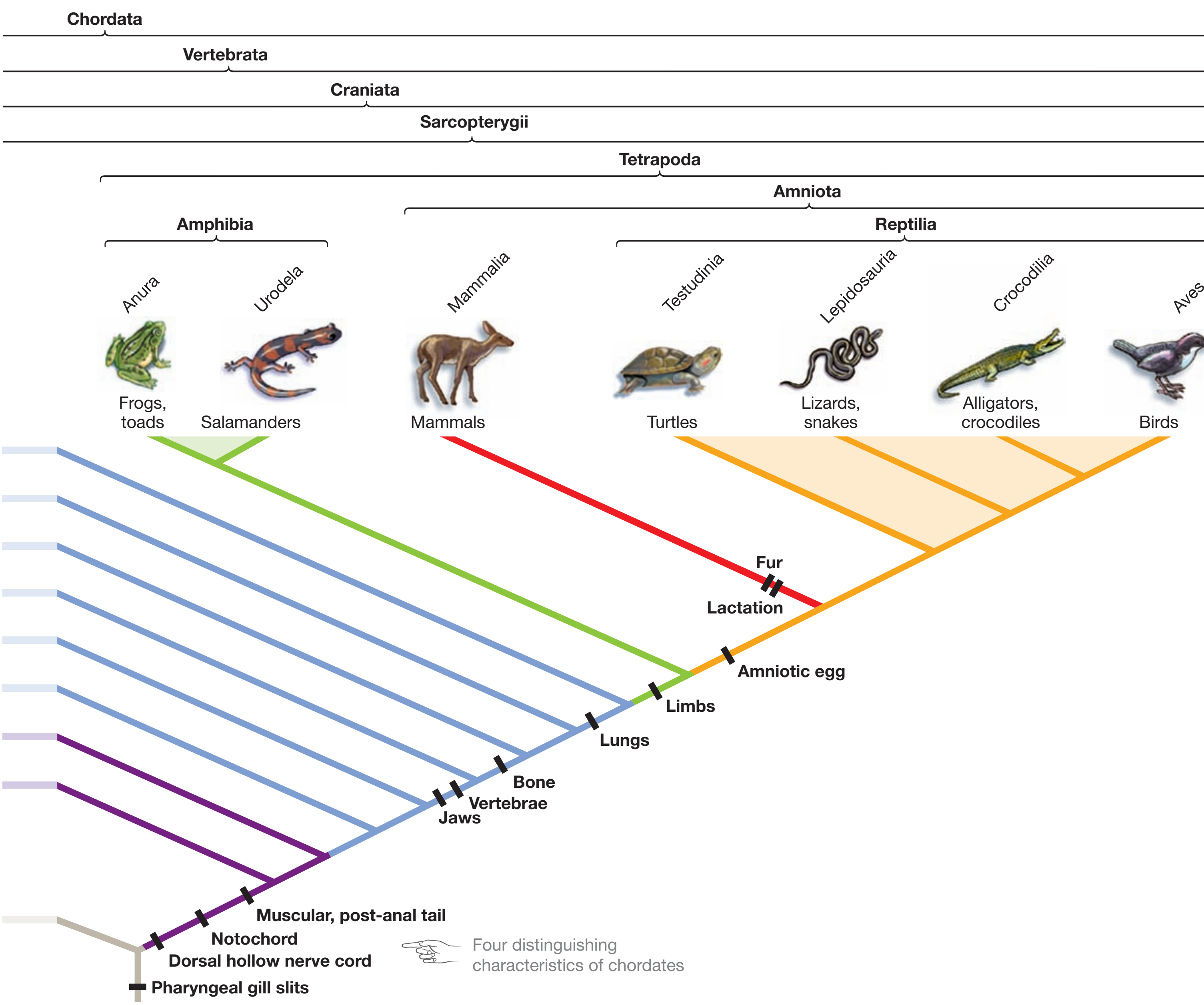
QUESTION Which group is more closely related to the amphibians: mammals or birds?

- About 20 million years after the appearance of tetrapods in the fossil record, the first amniotes are present. The Amniota is a lineage of vertebrates that includes all tetrapods other than amphibians. The **amniotes** are named for a signature adaptation: the amniotic egg. An **amniotic egg** is an egg that has a watertight shell or case enclosing a membrane-bound food supply, water supply, and waste repository. The evolution of the amniotic egg was siFificant because it gave vertebrates the ability to reproduce far from water. Amniotic eggs resist drying out, so vertebrates that produce amniotic eggs do not have to return to aquatic habitats to lay their eggs.

To summarize, the fossil record indicates that vertebrates evolved through a series of major steps, beginning about 540 million years ago with vertebrates whose endoskeleton consisted of a notochord. The earliest vertebrates gave rise to cartilaginous fishes (sharks and rays) and fish with bony skeletons and jaws. After the tetrapods emerged and amphibians resembling salamanders began to live on land, the evolution of the amniotic egg paved the way for the evolution of the first truly terrestrial vertebrates. The fossil record indicates that a radiation of reptiles followed, along with the animals that gave rise to mammals. Do phylogenetic trees estimated from analyses of DNA sequence data agree or conflict with these conclusions?

Evaluating Molecular Phylogenies

Figure 34.7 provides a phylogenetic tree that summarizes the relationships among vertebrates, based on DNA sequence data. The labelled bars on the tree indicate where major innovations occurred. Although the phylogeny of deuterostomes continues to be a topic of intense research, researchers are increasingly



confident that the relationships described in Figure 34.7 are accurate. Box 34.1 on page 777 discusses some of the implications of this tree, in terms of how lineages on the tree of life are named.

The overall conclusion from this tree is that the branching sequence inferred from morphological and molecular data correlates with the sequence of groups in the fossil record. Reading up from the base of the tree, it is clear that the closest living relatives of the vertebrates are the cephalochordates. The most basal groups of chordates lack the skull and vertebral column that define the vertebrates, and the most ancient lineages of vertebrates lack jaws and bony skeletons. You should be able to indicate the origin of the cranium on Figure 34.7.

To understand what happened during the subsequent diversification of echinoderms and vertebrates, let's explore some of the major innovations involved in feeding, movement, and reproduction in more detail.

Check Your Understanding

If you understand that...

- The fossil record documents a series of innovations that occurred as vertebrates diversified, including a cartilaginous skeleton, bone, jaws, limbs, and a membrane-bound egg.

You should be able to...

1) Explain how each of these innovations allowed vertebrates to move, find food, or reproduce efficiently.
2) Indicate the origin of each of these key traits on a phylogenetic tree of vertebrates.

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Deuterostome Diversity

34.3 What Themes Occur in the Diversification of Deuterostomes?

In terms of numbers of species and range of habitats occupied, the most successful lineages of deuterostomes are the echinoderms, with 7000 named species, and the vertebrates, with 54 000 known species. Echinoderms are widespread and abundant in marine habitats. In some deepwater environments, echinoderms represent 95 percent of the total mass of organisms. Among vertebrates, the most species-rich and ecologically diverse lineages are the ray-finned fishes and the tetrapods (**Figure 34.8**). Ray-finned fishes occupy habitats ranging from deepwater environments, which are perpetually dark, to shallow ponds that dry up each year. Tetrapods include the large herbivores and predators in terrestrial environments all over the world.

Today there are about 7000 species of echinoderms, about 27 000 species of ray-finned fish, and about 27 000 species of

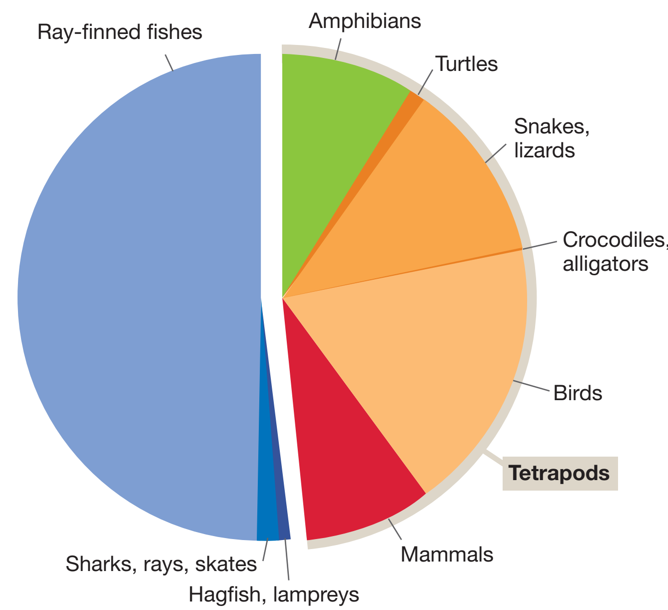


FIGURE 34.8 Relative Species Abundance Among Vertebrates.

tetrapods. To understand why these lineages have been so successful, it's important to recognize that they have unique body plans. Recall that echinoderms are radially symmetric and have a water vascular system, and that ray-finned fishes and tetrapods have a bony endoskeleton. In this light, the situation in deuterostomes appears to be similar to that in protostomes. Recall from Chapter 33 that the most evolutionarily successful protostome lineages are the arthropods and molluscs. A major concept in that chapter was that arthropods and molluscs have body plans that are unique among protostomes. Once their distinctive body plans evolved, evolution by natural selection led to extensive diversification based on novel methods for eating, moving, and reproducing.

Feeding

Animals eat to live, and it is logical to predict that each of the tens of thousands of echinoderm and vertebrate species eats different things in different ways. It is also logical to predict that echinoderms and vertebrates have traits that make diverse ways of feeding possible.

Both predictions are correct. Echinoderms have feeding strategies that are unique among marine animals. Many are based on the use of their water vascular system and podia. Ray-finned fishes and tetrapods, in contrast, depend on their jaws.

How Do Echinoderms Feed? Depending on the lineage and species in question, echinoderms make their living by suspension feeding, deposit feeding, or harvesting algae or other animals. In most cases, an echinoderm's podia play a key role in obtaining food. Many sea stars, for example, prey on bivalves. Clams and mussels respond to sea star attacks by contracting muscles that close their shells tight. But by clamp-

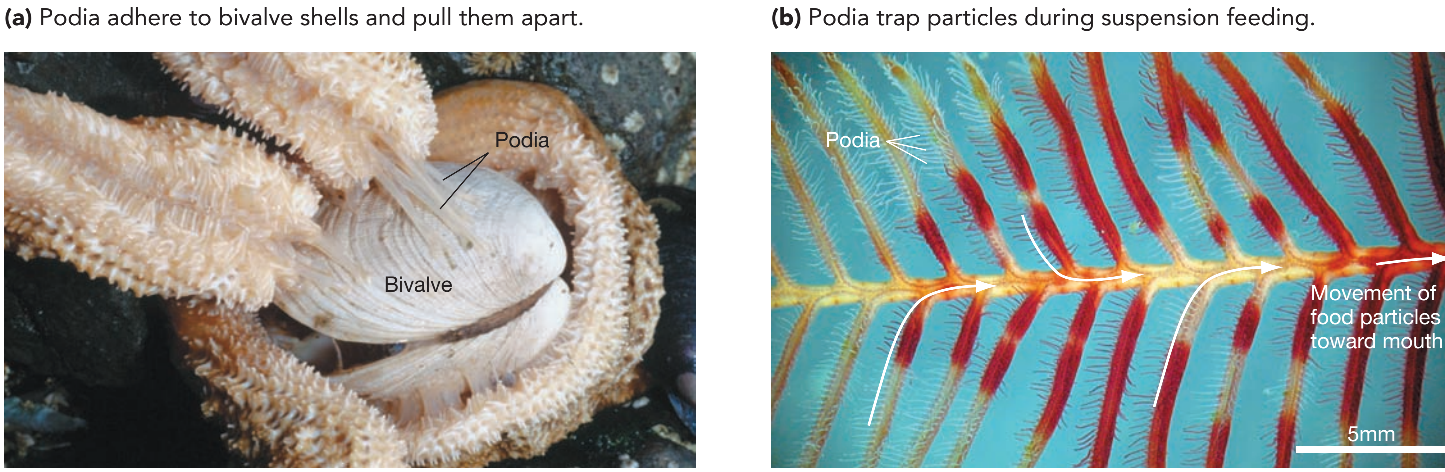


FIGURE 34.9 Echinoderms Use Their Podia in Feeding. (a) A sea star pries open a bivalve slightly and then everts its stomach into the bivalve to digest it. **(b)** Feather stars extend their podia when they suspension feed.

ing onto each shell with their podia and pulling, sea stars are often able to pry the shells apart a few millimetres (**Figure 34.9a**). Once a gap exists, the sea star extrudes its stomach from its body and forces the stomach through the opening between the bivalve's shells. Upon contacting the visceral mass of the bivalve, the stomach of the sea star secretes digestive enzymes. It then begins to absorb the small molecules released by enzyme action. Eventually, only the unhinged shells of the prey remain.

Podia are also involved in echinoderms that suspension feed (**Figure 34.9b**). In most cases, podia are extended out into the water. When food particles contact them, the podia flick the food down to cilia, which sweep the particles toward the animal's mouth. In deposit feeders, podia secrete mucus that is used to sop up food material on the substrate. The podia then roll the food-laden mucus into a ball and move it to the mouth.

The Vertebrate Jaw The most ancient groups of vertebrates have relatively simple mouthparts. For example, hagfish and lampreys lack jaws and cannot bite algae, plants, or animals. They have to make their living as ectoparasites or as deposit feeders that scavenge dead animals.

Vertebrates were not able to harvest food by biting until jaws evolved. The leading hypothesis for the origin of the jaw proposes that natural selection acted on mutations that affected the morphology of **gill arches**, which are curved regions of tissue between the gills. The jawless vertebrates have bars of cartilage that stiffen these gill arches. The gill-arch hypothesis proposes that mutation and natural selection increased the size of an arch and modified its orientation slightly, producing the first working jaw (**Figure 34.10**). Three lines of evidence, drawn from comparative anatomy and embryology, support the gill-arch hypothesis:

1. Both gill arches and jaws consist of flattened bars of bony or cartilaginous tissue that hinges and bends forward.

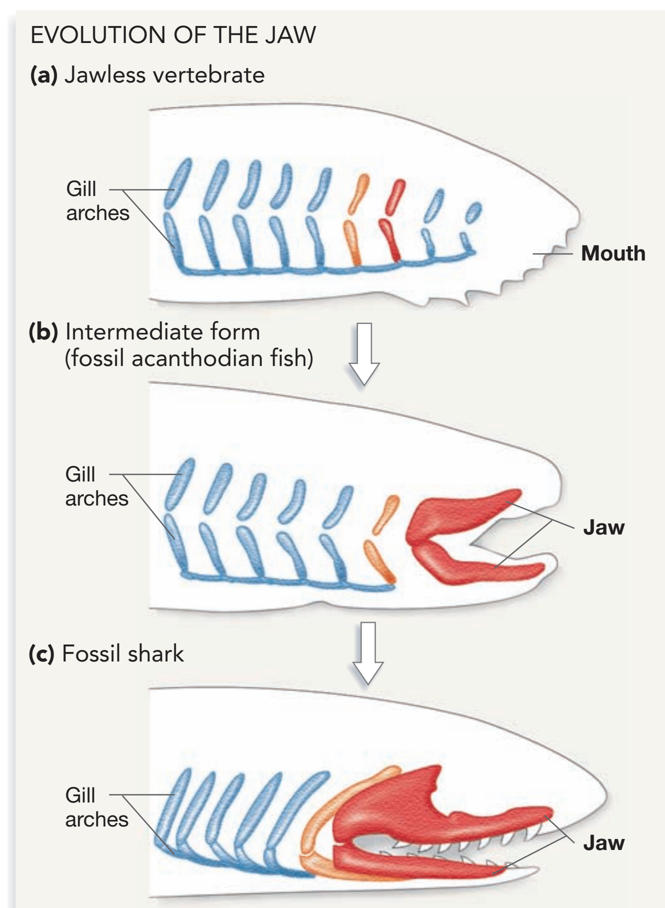


FIGURE 34.10 A Hypothesis for the Evolution of the Jaw. (a) Gill arches support the gills in jawless vertebrates. **(b)** In the fossil record, jawbones appear first in fossil fish called acanthodians. **(c)** Fossil sharks that appeared later had more elaborate jaws.

QUESTION The transition from gill arches to the jaws of acanthodian fishes is complex. Intermediate forms have yet to be found in the fossil record. Would intermediate stages in the evolution of the jaw have any function?

2. During development, the same population of cells gives rise to the muscles that move jaws and the muscles that move gill arches.
3. Unlike most other parts of the vertebrate skeleton, both jaws and gill arches are derived from specialized cells in the embryo called neural crest cells.

Taken together, these data support the hypothesis that jaws evolved from gill arches.

To explain why ray-finned fishes are so diverse in their feeding methods, biologists point to important modifications of the jaw. In most ray-finned fishes, for example, the jaw is protrusible—meaning it can be extended to nip or bite out at food. In addition, several particularly species-rich lineages of ray-finned fishes have a set of pharyngeal jaws. The **pharyngeal** ("throat") **jaw** consists of modified gill arches that function as a second set of jaws, located in the back of the mouth. Pharyngeal jaws are important because they make food processing particularly efficient. (For more on the structure and function of pharyngeal jaws, see Chapter 43.)

To summarize, the radiation of ray-finned fishes was triggered in large part by the evolution of the jaw, by modifications that made it possible to protrude the jaw, and by the origin of the pharyngeal jaw. The story of tetrapods is different, however. Although jaw structure varies somewhat among tetrapod groups, the adaptation that triggered their initial diversification involved the ability to get to food, not to bite it and process it.

Movement

The signature adaptations of echinoderms and tetrapods involve locomotion. We've already explored the water vascular system and tube feet of echinoderms; here let's focus on the tetrapod limb.

Most tetrapods live on land and use their limbs to move. But for vertebrates to succeed on land, they had to be able not only to move out of water but also to breathe air and avoid drying out. To understand how this was accomplished, consider the morphology and behaviour of their closest living relatives, the lungfish (**Figure 34.11**). Most living species of lungfish inhabit shallow, oxygen-poor water. To supplement the oxygen taken in by their gills, they have lungs and breathe air. Some also have fleshy fins supported by bones and are capable of walking short distances along watery mudflats or the bottoms of ponds. In addition, some species can survive extended droughts by burrowing in mud.

Fossils provide strong links between lungfish and the earliest land-dwelling vertebrates. **Figure 34.12** shows three of the species involved. The first, an aquatic animal related to today's lungfishes, is from the Devonian period—about 382 million years ago. The second is one of the oldest tetrapods, or limbed vertebrates, found to date. This animal appears in the fossil record about 365 million years ago. The third is a more recent tetrapod fossil, dated to about 350 million years ago. The figure

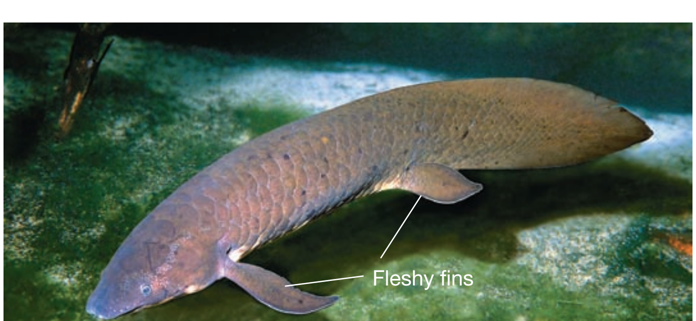


FIGURE 34.11 Lungfish Have Limb-like Fins. Some species of lungfish can walk or crawl short distances on their fleshy fins.

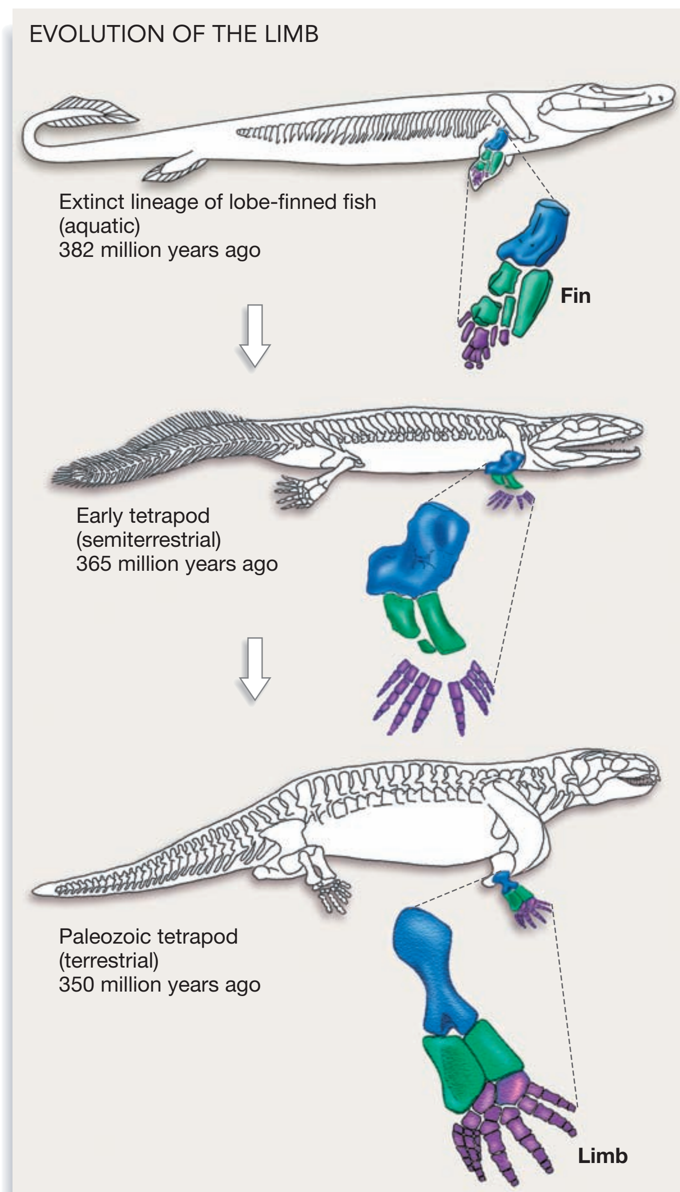


FIGURE 34.12 Fossil Evidence for a Fin-to-Limb Transition. The number and arrangement of bones in the fins and limbs of these fossil organisms agree with the general form of the modern tetrapod limb. The colour coding indicates homologous elements.

highlights the numbers and arrangement of bones in the fossil fish fin and the numbers and arrangement of bones in the limbs of early tetrapods. The colour coding emphasizes that each fin or limb has a single bony element that is proximal (closest to the body) and then two bones that are distal (farther from the body) and arranged side by side, followed by a series of distal elements. Because the structures are similar, and because no other animal groups have limb bones in this arrangement, the evidence for homology is strong. Based on the lifestyle of living lungfish, biologists suggest that mutation and natural selection gradually transformed fins into limbs as the first tetrapods became more and more dependent on terrestrial habitats.

The hypothesis that tetrapod limbs evolved from fish fins has also been supported by molecular genetic evidence. Recent work has shown that several regulatory proteins involved in the development of zebrafish fins and the upper parts of mouse limbs are homologous. Specifically, the proteins produced by several different *Hox* genes are found at the same times and in the same locations in fins and limbs. These data suggest that these appendages are patterned by the same genes. As a result, the data support the hypothesis that tetrapod limbs evolved from fins.

Once the tetrapod limb evolved, natural selection elaborated it into structures that are used for running, gliding, crawling, burrowing, or swimming. In addition, wings and the ability to fly evolved independently in three lineages of tetrapods: the extinct flying reptiles called pterosaurs (pronounced *TARE-oh-sors*), birds, and bats. Tetrapods and insects are the only animals that have taken to the skies. **Box 34.2** explores how flight evolved in birds.

To summarize, the evolution of the jaw gave tetrapods the potential to capture and process a wide array of foods. With limbs, they could move efficiently on land in search of food. What about the other major challenge of terrestrial life? How did tetrapods produce offspring that could survive out of water?

BOX 34.2 The Evolution of Flight in Birds

In 2003 Xing Xu and colleagues announced the discovery of a spectacular fossilized dinosaur called *Microraptor gui*. As **Figure 34.13** shows, *M. gui* had feathers covering its wings, body, and legs. But as impressive as it is, *M. gui* was just one in an exciting series of feathered dinosaur species unearthed by Xu's group. Taken together, the newly discovered species answer several key questions about the evolution of birds, feathers, and flight:

FIGURE 34.13 Feathers Evolved in Dinosaurs. An artist's depiction of what *Microraptor gui*, a dinosaur that had feathers on its body and all four limbs, might have looked like in life.

- *Did birds evolve from dinosaurs?* On the basis of skeletal characteristics, all of these recently discovered fossil species clearly belong to a lineage of dinosaurs called the dromaeosaurs. The fossils definitively link the dromaeosaurs and the earliest known fossil birds.
- *How did feathers evolve?* The fossils support Xu's model that feathers evolved in a series of steps, beginning with simple projections from the skin and culminating with the complex structures observed in today's birds (**Figure 34.14**). *M. gui*, for example, had two distinct types of feathers but lacked the complex feathers found in contemporary birds. It is controversial, though, whether the original function of feathers was for courtship, other types of display, or insulation. In today's birds, feathers function in display, insulation, and flight.
- *Did birds begin flying from the ground up or from the trees down?* More specifically, did flight evolve with running species that began to jump and glide or make short flights, with the aid of feathers to provide lift? Or did flight evolve from tree-dwelling species that used feathers to glide from tree to tree, much as flying squirrels do today? Because it is unlikely that *M. gui* could run efficiently with feathered legs, Xu and colleagues propose that flight evolved from tree-dwelling gliders. A recent analysis suggests that *M. gui* used all four of its feathered limbs as wings, in a biplane-like arrangement that made gliding particularly efficient.

Once dinosaurs evolved feathers and took to the air as gliders, the fossil record shows that a series of adaptations made powered, flapping flight increasingly efficient. Although most dinosaurs have a flat sternum (breastbone), the same structure in birds has an elongated projection

continued

called the keel, which provides a large surface area to which flight muscles attach (**Figure 34.15**; note that on a chicken or turkey, the flight muscles are called "breast meat"). Birds are also extraordinarily light for their size, primarily because they have a drastically reduced number of bones and because their larger bones are thin-walled and hollow—though strengthened by bony "struts" (see Figure 34.15). Birds are also capable of long periods of sustained activity year-round, because they are **endotherm**—meaning that they maintain a high body temperature by producing heat in their tissues. From dinosaurs that jumped and glided from tree to tree, birds have evolved into extraordinary flying machines.

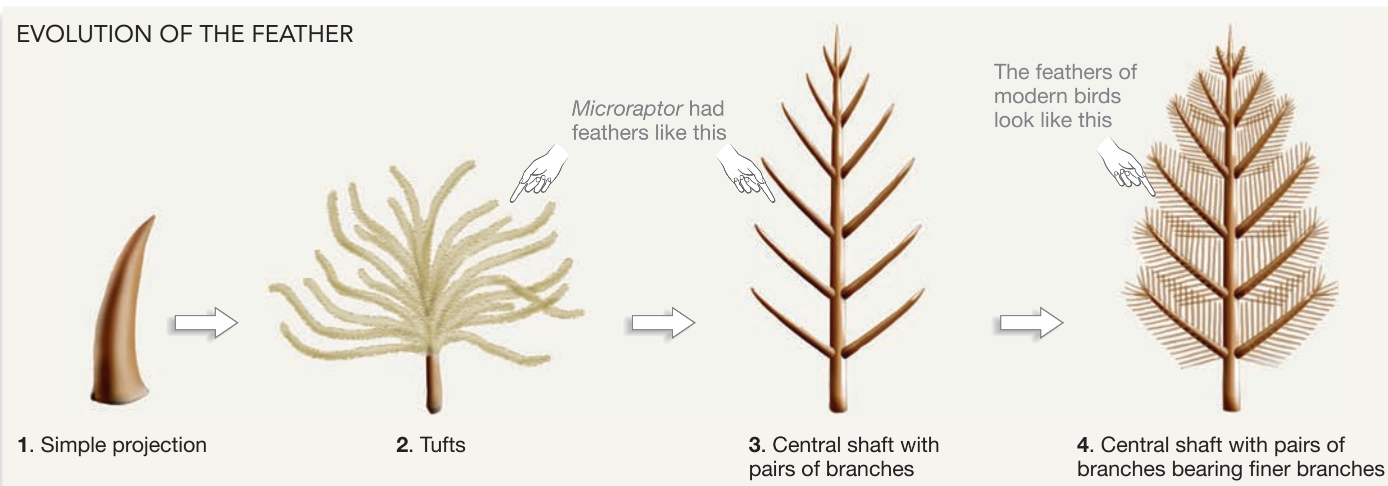


FIGURE 34.14 Feathers Evolved through Intermediate Stages. This model for the evolution of feathers is supported by the fossil record.

QUESTION Suggest a function for simple projections and tufts in the ancestors of birds, prior to the evolution of more complex feathers that made gliding or flapping flight possible.

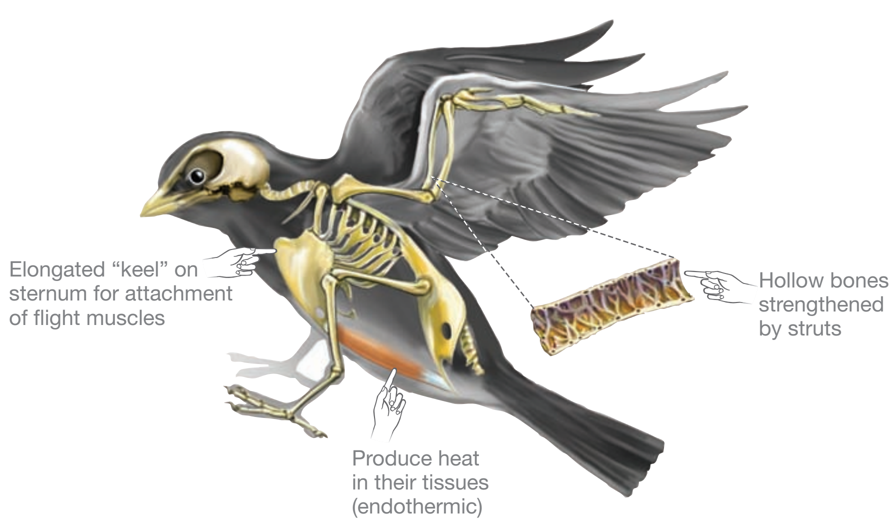


FIGURE 34.15 In Addition to Feathers, Birds Have Several Adaptations That Allow for Flight.

Reproduction

Among the various lineages of fish, a few species undergo only asexual reproduction. When sexual reproduction occurs, it may be based on internal or external fertilization and oviparity, viviparity, or ovoviviparity. In addition, parental care is extensive in some fish species, and it often involves guarding eggs from predators and fanning them to keep oxygen levels high. All fish lay their eggs or give birth in water, however. Tetrapods were the first vertebrates that were able to breed on land.

Three major evolutionary innovations gave tetrapods the ability to produce offspring successfully in terrestrial environments: (1) the amniotic egg, (2) the placenta, and (3) elaboration of parental care. Let's explore each of these innovations in turn.

What Is an Amniotic Egg? Amniotic eggs have shells that minimize water loss as the embryo develops inside. The first tetrapods, like today's amphibians (frogs, toads, and salamanders), lacked amniotic eggs. Although their eggs were encased by a membrane, the first tetrapods laid eggs that would dry out and die unless they were laid in water. This fact limited the range of habitats these animals could exploit. Like today's amphibians, the early tetrapods were largely restricted to living in or near marshes, lakes, or ponds.

In contrast, reptiles (including birds) and the egg-laying mammals produce amniotic eggs. The outer membrane of the amniotic egg is leathery in turtles, snakes, and lizards but hard—due to deposition of calcium carbonate—in crocodiles, birds, and the egg-laying mammals. Besides having an outer shell or membrane that is largely watertight, an amniotic egg contains a membrane-bound supply of water in a protein-rich solution called **albumen** (**Figure 34.16**). The embryo itself is enveloped in a protective inner membrane known as the **amnion**. Inside an amniotic egg, the embryo is bathed in fluid. The egg itself is highly resistant to drying.

The evolution of the amniotic egg was a key event in the diversification of tetrapods because it allowed turtles, snakes, lizards, crocodiles, birds, and the egg-laying mammals to reproduce in any terrestrial environment—even habitats as dry as deserts. Members of the lineage called Amniota now occupy all types of terrestrial environments. But during the evolution of mammals, a second major innovation in reproduction occurred that eliminated the need for any type of egg laying: the placenta.

The Placenta Recall from Chapter 32 that egg-laying animals are said to be **oviparous**, while species that give birth are termed **viviparous**. In many viviparous animals, females produce an egg that contains a nutrient-rich yolk. Instead of laying the egg, however, the mother retains it inside her body. In these **ovoviviparous** species, the developing offspring depends on the resources in the egg yolk. In most mammals, however, the eggs that females produce lack yolk. After fertilization occurs and the egg is retained, the mother produces a placenta within her uterus. The **placenta** is an organ that is rich in blood vessels and that facilitates a flow of oxygen and nutrients from the mother to the developing offspring (**Figure 34.17**). After a development period called **gestation**, the embryo emerges from the mother's body.

Why did viviparity and the placenta evolve? Biologists have formulated an answer to this question by pointing out that females have a finite amount of time and energy available to invest in reproduction. As a result, a female can produce a large number of small offspring or a small number of large offspring but not a large number of large offspring. Stated more formally, every female faces a **trade-off**—an inescapable compromise—between the quantity of offspring she can produce and their size. In some lineages, natural selection has favoured traits that allow females to produce a small number of large, well-developed offspring. Viviparity and the placenta are two such traits. Compared with female insects or echinoderms, which routinely lay thousands or even millions of eggs over the course of a lifetime, a female mammal produces just a few offspring. But because those offspring are protected inside her body and fed until they are well developed, they are much more likely to survive than sea star or insect embryos are. Even after the birth of their young, many mammals continue to invest time and energy in rearing them.

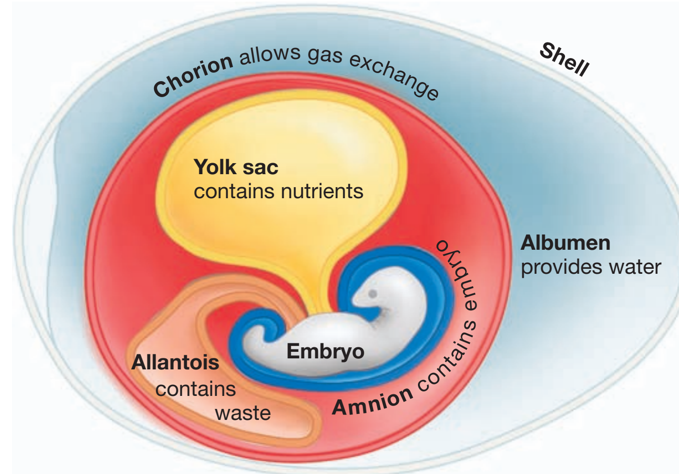


FIGURE 34.16 An Amniotic Egg. Amniotic eggs have membrane-bound sacs that hold nutrients, water, and waste and that allow gas exchange.

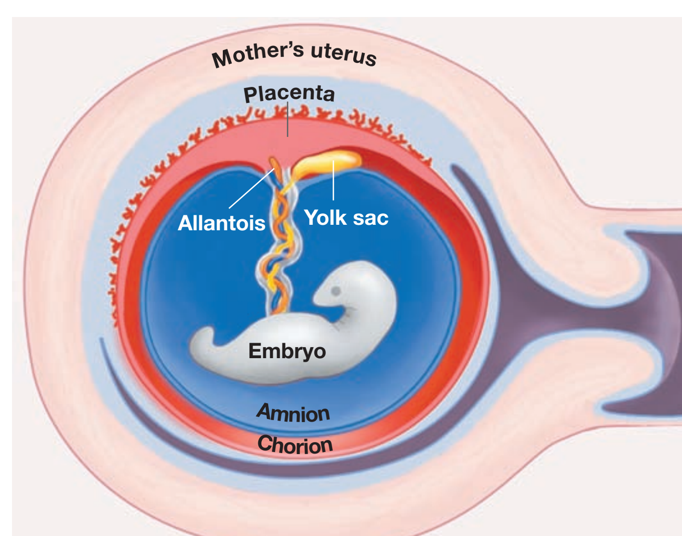


FIGURE 34.17 The Placenta Allows the Mother to Nourish the Fetus Internally.

QUESTION Compare the relative positions of the chorion and amnion here with those in the amniotic egg (Figure 34.16). Are they the same or different?

Parental Care The term **parental care** encompasses any action by a parent that improves the ability of its offspring to survive, including incubating eggs to keep them warm during early development, keeping young warm and dry, supplying young with food, and protecting them from danger. In some insect and frog species, mothers carry around eggs or newly hatched young; in fishes, parents commonly guard eggs during development and fan them with oxygen-rich water.

The most extensive parental care observed among animals is provided by mammals and birds. In both groups, the mother and often the father continue to feed and care for individuals after birth or hatching—sometimes for many years (**Figure 34.18**). Female mammals also **lactate**—meaning that they produce a nutrient-rich fluid called milk and use it to feed their offspring after birth. With the combination of the placenta and lactation, placental mammals make the most extensive investment of time and energy in offspring known. Among large animals, the evolution of extensive parental care is hypothesized to be a major reason for the evolutionary success of mammals and birds.

(a) Mammal mothers feed and protect newborn young.

(b) Many bird species have extensive parental care.

FIGURE 34.18 Parental Care in Mammals and Birds. (a) Female mammals feed and protect embryos inside their bodies until the young are well developed. Once the offspring is born, the mother feeds it milk until it is able to eat on its own. In some species, parents continue to feed and protect young for many years. **(b)** In birds, one or both parents may incubate the eggs, protect the nest, and feed the young after hatching occurs.

Check Your Understanding

If you understand that…

- Echinoderms and vertebrates have distinctive body plans. Subsequent diversification in each lineage was based on innovations that made it possible for species to feed, move, and reproduce in novel ways. Most echinoderms use their podia to move, but they feed in a wide variety of ways—including using their podia to pry open bivalves, suspension feed, or deposit feed.
- An array of key innovations occurred during the evolution of vertebrates: Jaws made it possible to bite and process food, limbs allowed tetrapods to move on land, and amniotic eggs could be laid on land.

You should be able to…

1) Summarize the leading hypotheses to explain how the jaw and limb evolved.
2) Diagram the structure of an amniotic egg.
3) Explain the role of increased parental care in the evolution of birds and mammals.

34.4 Key Lineages: Echinodermata

The echinoderms ("spiny-skins") were named for the spines or spikes observed in many species. They are bilaterally symmetric as larvae but undergo metamorphosis and develop into radially symmetric adults. As adults they all have a water vascular system and produce calcium carbonate plates in their skin to form an endoskeleton.

The echinoderms living today make up five major lineages, traditionally recognized as classes: (1) feather stars and sea lilies, (2) sea stars, (3) brittle stars and basket stars, (4) sea urchins and sand dollars, and (5) sea cucumbers (**Figure 34.19**). Most feather stars and sea lilies are sessile suspension feeders. Brittle stars and basket stars have five or more long arms that radiate out from a small central disk. They use these arms to suspension feed, deposit feed by sopping up material with mucus, or capture small prey animals. Sea cucumbers are sausage-shaped animals that suspension feed or deposit feed with the aid of modified tube feet called tentacles that are arranged in a whorl around their mouths. Sea stars, sea urchins, and sand dollars are described in detail in the text that follows.

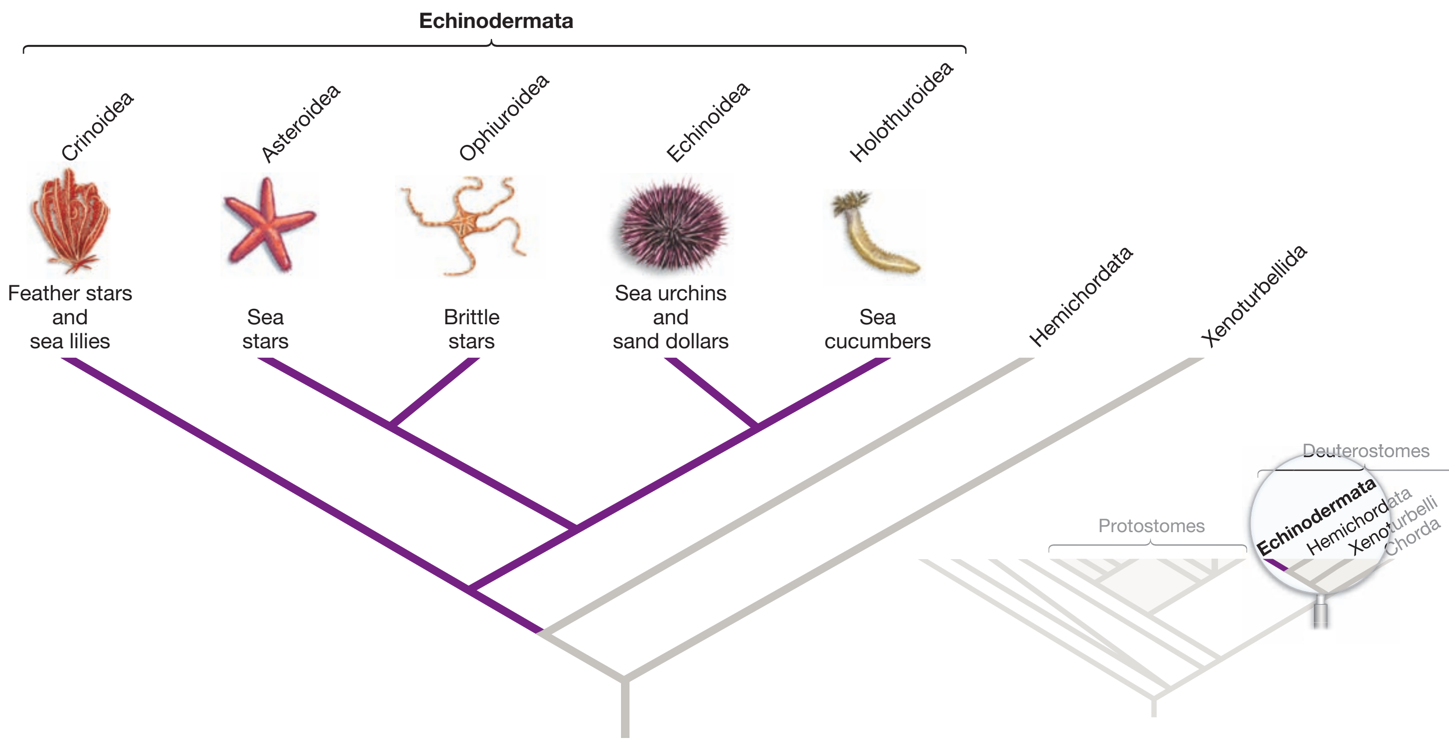


FIGURE 34.19 There Are Five Major Lineages of Echinoderms.

Echinodermata > Asteroidea (Sea Stars)

The 1700 known species of sea stars have bodies with five or more long arms—in some species up to 40—radiating from a central region that contains the mouth, stomach, and anus (**Figure 34.20**). Unlike brittle stars, though, the sea star's arms are not set off from the central region by clear, joint-like articulations. ● You should be able to indicate the origin of five arms, continuous with the central region, on Figure 34.19.

When fully grown, sea stars can range in size from less than 1 cm in diameter to 1 m across. They live on hard or soft substrates along the coasts of all the world's oceans. Although the spines that are characteristic of some echinoderms are reduced to knobs on the surface of most sea stars, the crown-of-thorns star and a few other species have prominent, upright, movable spines.

Feeding Sea stars are predators or scavengers. Some species pull bivalves apart with their tube feet and evert their stomach into the prey's visceral mass. Sponges, barnacles, and snails are also common prey. The crown-of-thorns sea star specializes in feeding on corals and is native to the Indian Ocean and western Pacific Ocean. Its population has skyrocketed recently—possibly because people are harvesting its major predator, a large snail called the triton, for its pretty shell. Large crown-of-thorns star populations have led to the destruction of large areas of coral reef.

Movement Sea stars crawl with the aid of their tube feet. Usually one of the five or more arms is used as the front or leading appendage as the animal moves.

Reproduction Sexual reproduction predominates in sea stars, and sexes are separate. At least one sea star arm is filled with reproductive organs that produce massive amounts of gametes—millions of eggs per female, in some species. Species that are native to habitats in the far north, where conditions are particularly harsh, care for their offspring by holding fertilized eggs on their body until the eggs hatch. Most sea stars are capable of regenerating arms that are lost in predator attacks or storms. Some species can reproduce asexually by dividing the body in two, with each of the two individuals then regenerating the missing half.

Pycnopodia helianthoides

FIGURE 34.20 Sea Stars May Have Many Arms.

Echinodermata > Echinoidea (Sea Urchins and Sand Dollars)

There are about 800 species of echinoids living today; most are sea urchins or sand dollars. Sea urchins have globe-shaped bodies and long spines and crawl along substrates (**Figure 34.21a**). Sand dollars are flattened and disk-shaped, have short spines, and burrow in soft sediments (**Figure 34.21b**). You should be able to indicate the origin of globular or disc-shaped bodies on Figure 34.19.

Feeding Sand dollars use their mucus-covered podia to collect food particles in sand or in other soft substrates. Most types of sea urchins are herbivores. In some areas of the world, urchins are extremely important grazers on kelp and other types of algae. In fact, when urchin populations are high, their grazing can prevent the formation of kelp forests. Most echinoids have a unique, jaw-like feeding structure in their mouths that is made up of five calcium carbonate teeth attached to muscles. In many species, this apparatus can extend and retract as the animal feeds.

Movement Using their podia, sea urchins crawl and sand dollars burrow. Sea urchins can also move their spines to aid in crawling along a substrate.

(a) Sea urchin *Echinus tylodes*

(b) Sand dollar *Dendraster excentricus*

FIGURE 34.21 Sea Urchins and Sand Dollars Are Closely Related.

Reproduction Sexual reproduction predominates in sea urchins and sand dollars. Fertilization is external, and sexes are separate.

34.5 Key Lineages: Chordata

The chordates comprise three major subgroups or subphyla: (1) the urochordates (also called tunicates, or sea squirts and salps), (2) the cephalochordates (lancelets), and (3) the craniates and vertebrates (**Figure 34.22**). There are about 1600 species of tunicates, 24 species of lancelets, and over 50 000 vertebrates. At some stage in their life cycle, all species in the phylum Chordata have a dorsal hollow nerve cord, a notochord, pharyngeal gill slits, and a muscular tail that extends past the anus.

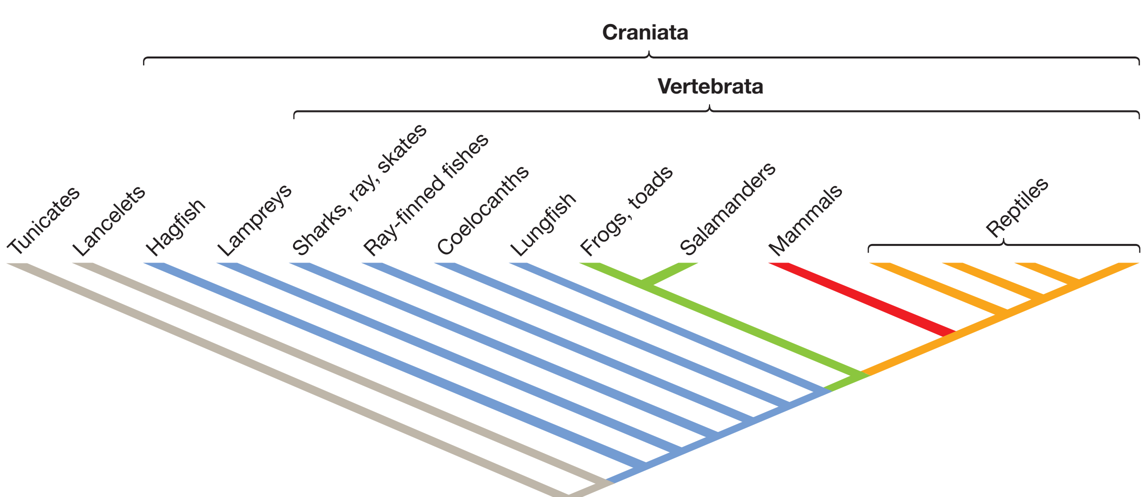


FIGURE 34.22 Craniates and Vertebrates Are Monophyletic Groups. All vertebrates are craniates, but not all craniates are vertebrates.

EXERCISE Draw a brace at the top of the tree to indicate which groups belong to the Chordata.

Chordata > Urochordata (Tunicates)

The urochordates are also called called tunicates; the two major subgroups are known as the sea squirts (or ascidians) and salps. All of the approximately 300 species described to date live in the ocean. Sea squirts live on the ocean floor (**Figure 34.23a**), while salps live in open water (**Figure 34.23b**).

The distinguishing characters of urochordates include an exoskeleton-like coat of polysaccharide, called a tunic, that covers and supports the body; a U-shaped gut; and two openings, called siphons, where water enters and leaves an individual during feeding. ● You should be able to indicate the origin of the tunic, siphons, and the U-shaped gut on Figure 34.22.

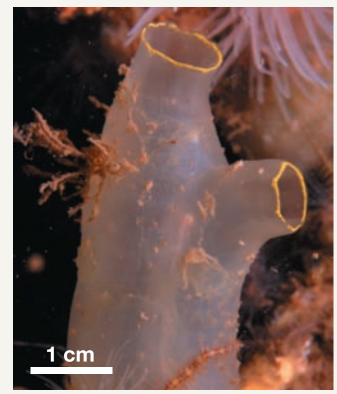
Feeding Adult urochordates use their pharyngeal gill slits to suspension feed. The slits trap particles present in the water that enters one siphon and leaves through the other siphon.

Movement Larvae swim with the aid of the notochord, which stiffens the body and functions as a simple endoskeleton. Larvae are a dispersal stage and do not feed. Adults are sessile or float in currents.

Reproduction In most species, individuals produce both sperm and eggs. In some species, both sperm and eggs are shed into the water and fertilization is external; in other species, sperm are released into the water but eggs are retained, so that fertilization and early development are internal. Asexual reproduction by budding is also common in some groups.

(a) Sea squirt

Ciona intestinalis



(b) Salp

Salpa fusiformis

FIGURE 34.23 Sea Squirts and Salps Live in Different Habitats.

Chordata > Cephalochordata (Lancelets)

About two dozen species of cephalochordates have been described to date, all of them found in marine sands. Lancelets—also called amphioxus—have several characteristics that are intermediate between invertebrates and vertebrates. Chief among these is a notochord that is retained in adults, where it functions as an endoskeleton. ● You should be able to indicate the origin of the notochord that is retained in adults on Figure 34.22.

Feeding Adult cephalochordates feed by burrowing in sediment until only their head is sticking out into the water. They take water in through their mouth and trap food particles with the aid of their pharyngeal gill slits.

Movement Adults have large blocks of muscle arranged in a series along the length of the notochord. Lancelets are efficient swimmers because the flexible, rod-like notochord stiffens the body, making it wriggle when the blocks of muscle contract (**Figure 34.24**).

Reproduction Asexual reproduction is unknown, and individuals are either male or female. Gametes are released into the environment and fertilization is external.

Branchiostoma lanceolatum

FIGURE 34.24 Lancelets Look like Fish but Are Not Vertebrates.

Chordata > Craniata > Myxinoidea (Hagfish) and Petromyzontoidea (Lampreys)

Although recent phylogenetic analyses indicate that hagfish and lampreys may belong to two independent lineages, some data suggest that they are a single group called the Agnatha ("not-jawed"). Because these animals are the only vertebrates that lack jaws, the 110 species in the two groups are still referred to as the jawless fishes. The hagfish and lampreys are the only surviving members of the earliest branches at the base of the vertebrates.

Hagfish and lampreys have long, slender bodies and are aquatic. Most species are less than a metre long when fully grown. Hagfish lack any sort of vertebral column, but lampreys have small pieces of cartilage along the length of their dorsal hollow nerve cord. Both hagfish and lampreys have brains protected by a cranium, as do the vertebrates. You should be able to indicate the origin of the cranium on Figure 34.22.

Feeding Hagfish are scavengers and predators (**Figure 34.25a**). They deposit feed on the carcasses of dead fish and whales, and some are thought to burrow through ooze at the bottom of the ocean, feeding on polychaetes and other buried prey. Lampreys, in contrast, are ectoparasites. They attach to the sides of fish or other hosts by suction, then use spines in their mouth and tongue to rasp a hole in the side of their victim (**Figure 34.25b**). Once the wound is open, they suck blood and other body fluids.

Movement Hagfish and lampreys have a well-developed notochord and swim by making undulating movements. Lampreys can also move themselves upstream, against the flow of water, by attaching their suckers to rocks and looping the rest of their body forward, like an inchworm. Although lampreys have fins that aid in locomotion, they do not have the paired lateral appendages—meaning fins or limbs that emerge from each side—found in vertebrates.

(a) Hagfish

Eptatretus stoutii

(b) Lampreys feeding on fish

Petromyzon marinus

FIGURE 34.25 Hagfish and Lampreys Are Jawless Vertebrates.

Reproduction Virtually nothing is known about hagfish mating or embryonic development. Some lampreys live in freshwater; others are **anadromous**—meaning they spend their adult life in the ocean, but swim up streams to breed. Fertilization is external, and adults die after breeding once. Lamprey eggs hatch into larvae that look and act like lancelets. The larvae burrow into sediments and suspension feed for several years before metamorphosing into free-swimming adults.

Chordata > Vertebrata > Chondrichthyes (Sharks, Rays, Skates)

The 970 species in this lineage are distinguished by their cartilaginous skeleton (*chondrus* is the Greek word for cartilage), the presence of jaws, and the existence of paired fins. Paired fins were an important evolutionary innovation because they stabilize the body during rapid swimming—keeping it from pitching up or down, yawing to one side or the other, or rolling. You should be able to indicate the origin of paired fins—which are also found in other groups of fishlike organisms—on Figure 34.22.

Most sharks, rays, and skates are marine, though a few species live in freshwater. Sharks have streamlined, torpedo-shaped bodies and an asymmetrical tail—the dorsal portion is longer than the ventral portion (**Figure 34.26a**) In contrast, the dorsal–ventral plane of the body in rays and skates is strongly flattened (**Figure 34.26b**).

Feeding A few species of ray and shark suspension feed on plankton, but most species in this lineage are predators. Skates and rays lie on the ocean floor and ambush passing animals; electric rays capture their prey by stunning them with electric discharges of up to 200 volts. Most sharks, in contrast, are active hunters that chase down prey in open water and bite it. The larger species of sharks feed on large fish or marine mammals. Sharks are referred to as the "top predator" in many marine ecosystems, because they are at the top of the food chain—nothing eats them. Yet the largest of all sharks, the whale shark, is a suspension feeder. Whale sharks filter plankton out of water as it passes over their gills.

Movement Rays and skates swim by flapping their greatly enlarged pectoral fins. (Pectoral fins are located on the sides of

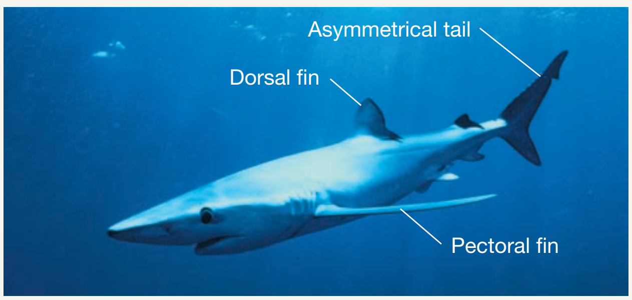
continued

Chordata > Vertebrata> Chondrichthyes (Sharks, Rays, Skates) *continued*

an organism; dorsal fins are located on the dorsal surface.) Sharks swim by undulating their bodies from side to side and beating their large tails.

Reproduction Sharks use internal fertilization, and fertilized eggs may be shed into the water or retained until the young are hatched and well developed. In some viviparous species, embryos are attached to the mother by specialized tissues in a mammal-like placenta, where the exchange of gases, nutrients, and wastes takes place. Skates are oviparous, but rays are viviparous.

(a) Sharks are torpedo shaped. *Prionace glauca*



(b) Skates and rays are flat. *Taeniura melanospila*

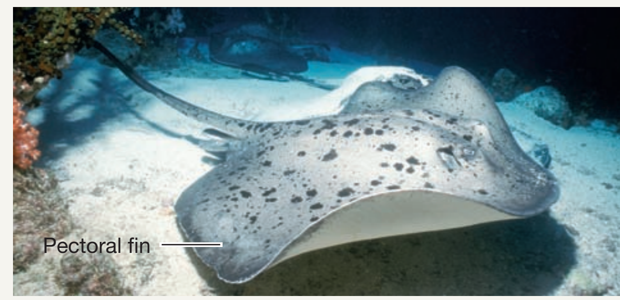


FIGURE 34.26 Sharks and Rays Have Cartilaginous Skeletons.

CANADIAN **RESEARCH** 34.1

The Decline of Large, Predatory Fishes in the World's Oceans

Humans have been fishing for millennia, selectively harvesting the largest fish from the seas. Technological advances in the last 50 years have greatly increased our ability to locate and capture fish: With radar, satellites, powerful harpoons, and huge nets, fishers are able to locate, track, and capture fish in the most remote parts of the ocean. Dalhousie University researchers Ransom A. Myers (**Figure A**) and Boris Worm set out to tally the effects of industrial fishing on large, predatory fish. They collected local and regional fishing records from around the world, searching through Japanese logbooks, trawling records from the Gulf of Thailand, and all other continuous fishing records from the 1950s to the present day. Trained as a mathematician and physicist, Myers was particularly well suited to analyze and extract trends from the huge sets of data.

In 2003, Myers and Worm published their shocking findings in the journal *Science*: The numbers of large, predatory fish in the world's oceans have dropped by 90 percent over the last 50 years. Myers summed it up: "From great blue marlin to mighty bluefin tuna, and from tropical groupers to Antarctic cod, industrial fishing has scoured the global ocean. There is no blue frontier left."

The Japanese longline fleet hunts fish in open ocean regions around the world. **Figure B** shows the decline in fish biomass recorded by the fleet. In the first 10 years of longline fishing, the overall success of the fleet fell from 6–12 fish to 0.5–2 fish per 100 hooks set. The increasing blue area on the map shows the advancing depletion of large fishes in all oceans. These trends are repeated whenever a new area is fished: Very high catch rates are recorded at first, but rates decline quickly over time. All areas in the world now have very low catch rates, and some formerly productive regions are no longer fished at all. In the first five years after commercial trawling operations began, the Gulf of Thailand lost 60 percent of its large fishes. The narrow continental shelf of South Georgia was fished out within two years.

Figure A *Dr. Ransom A. Myers, 1952–2007.*

The real declines in fish biomass are likely higher than those calculated by Myers and Worm. Reductions in fish abundance probably began before industrial times, as human populations and fishing pressure grew, and the 1950s data thus do not represent a baseline. As fisheries technology advances, fishers get more successful at catching the few remaining fish. As a result, today's low catch rates may overestimate current biomass of large fish.

continued

CANADIAN RESEARCH 34.1 (continued)

For a long time, humans have acted as though large marine fishes could not be fished to extinction. It was thought that fish were abundant, that many of them lived in remote areas where they were not vulnerable to human predation, and that they reproduced quickly when conditions were suitable. All of these assumptions have proven to be false. Today, the majority of the world's fisheries are fully exploited, overfished, or fished to exhaustion. Large, predatory fish are in decline throughout the world's oceans, even in remote areas. Sharks have been particularly hard-hit, with biomass reductions of over 99 percent in some species.

Unless fishing is reduced or halted and fisheries management improves, the extinction of large, predatory fishes is a very real possibility. Communities that depend on fishing may suffer food shortages and economic hardship. Marine ecosystems will be permanently altered. "Hunters have always been very good at killing big animals," said Myers. "Ten thousand years ago, with just some pointed sticks, humans managed to wipe out woolly mammoths, saber-toothed tigers, mastodons, and giant vampire bats. The same thing could happen to the oceans. We are in massive denial and continue to bicker over the last survivors, employing satellites and sensors to catch the last fish. We must act now, before they have reached the point of no return. If present fishing levels persist, these great fish will go the way of the dinosaurs."

The decline of large, predatory fishes with the rise of industrial fisheries has fundamentally changed marine ecosystems. Myers and his team explored the cascade of ecological effects that can be seen along the east coast of North America with the loss of the great sharks. Shark surveys have been conducted annually along the eastern seaboard since 1972. All species of great sharks (with adults over 2 m in length) have declined over this period, with losses ranging from 87 percent to over 99 percent. The decline is shown for six species of great sharks in the top row of graphs in **Figure C**. The largest individuals have suffered the greatest decline, with mean lengths decreasing by 17–47 percent, depending on species. Great sharks, formerly the top predators in this ecosystem, have been functionally eliminated.

The main prey of the great sharks is mid-sized sharks, skates, and rays. These fishes produce large eggs and large juveniles: too large to be eaten by anything except great sharks. With great sharks removed, these prey species have increased in abundance, as shown in the second row of graphs in Figure C. The result of the removal of great sharks has been a cascade of effects. Population numbers of several species, such as the cownose ray, have increased by an order of magnitude. Over 40 000 cownose rays now live—and feed—on the east coast of North America. The cownose ray feeds on bivalves: bay scallops, clams, and oysters. Several decades ago, field sampling showed no significant decline in numbers of bay scallops after the cownose ray migration. Recent sampling shows nearly complete loss of bay scallops due to predation by migrating rays. Only in enclosures built to exclude rays did bay scallop abundance stay high. In 2004, a century-old bay scallop fishery was closed down. Clams and oysters are also in decline.

Similar cascading effects are likely occurring in other areas affected by the loss of great sharks. Ocean ecosystems are being transformed, and we may not recognize the full extent of these effects until it is too late.

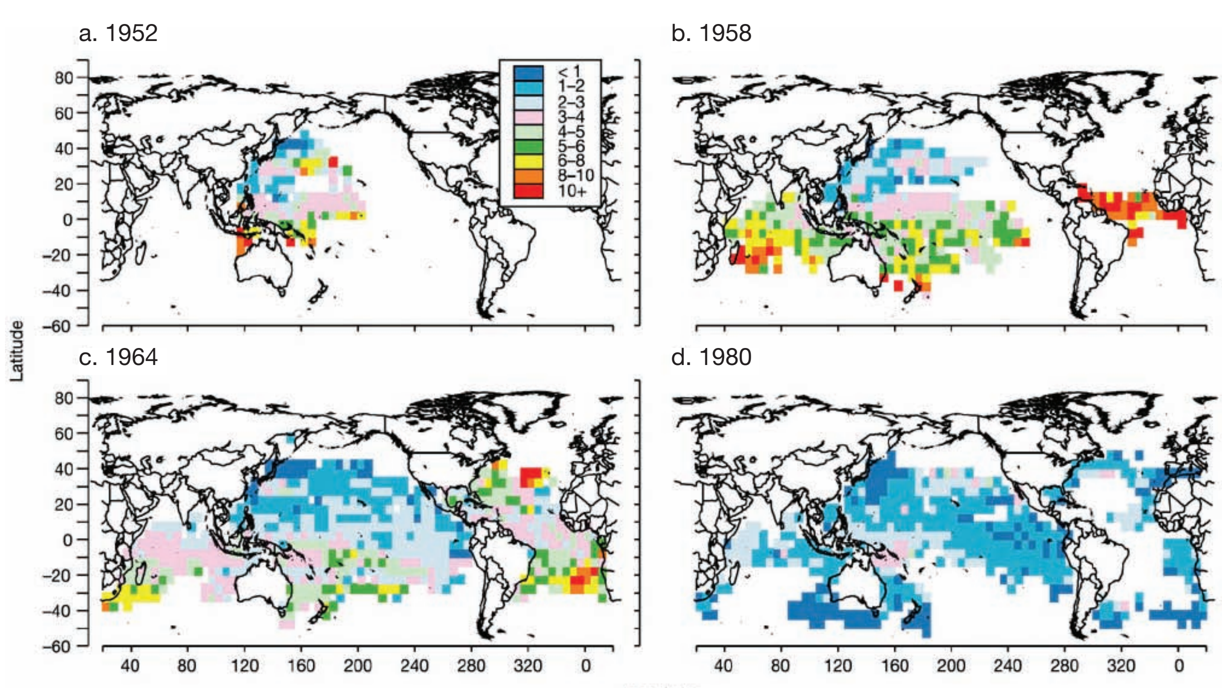


Figure B *Decreasing biomass of large, predatory fish under industrialized fishing pressure.*

CANADIAN RESEARCH 34.1 *(continued)*

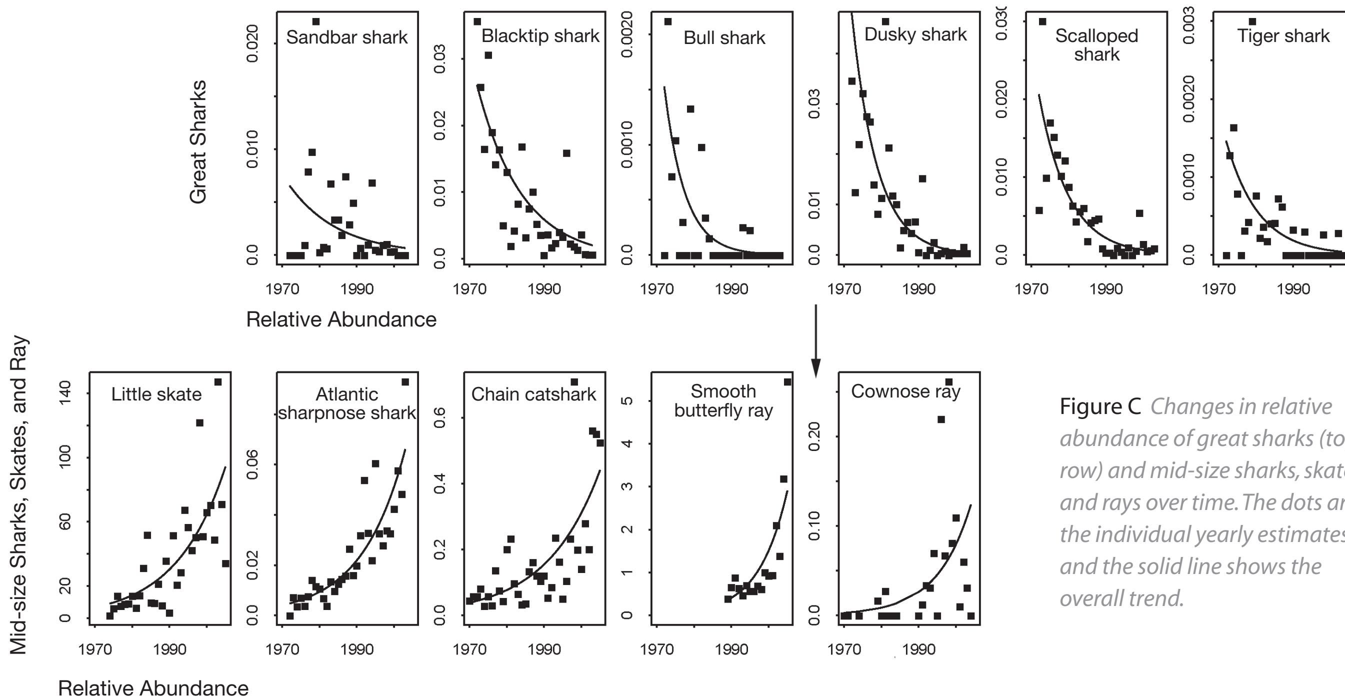


Figure C *Changes in relative abundance of great sharks (top row) and mid-size sharks, skates, and rays over time. The dots are the individual yearly estimates and the solid line shows the overall trend.*

Chordata > Vertebrata > Actinopterygii (Ray-Finned Fishes)

Actinopterygii (pronounced *ack-tin-op-teh-RIJ-ee-i*) means "ray-finned." Logically enough, these fish have fins that are supported by long, bony rods arranged in a ray pattern. They are the most ancient living group of vertebrates that have a skeleton made of bone. Their bodies are covered with interlocking scales that provide a stiff but flexible covering, and they have a gas-filled **swim bladder**. The evolution of the swim bladder was an important innovation because it allowed ray-finned fishes to avoid sinking. Tissues are heavier than water, so the bodies of aquatic organisms tend to sink. Sharks and rays, for example, have to swim to avoid sinking. But ray-finned fishes have a bladder that changes in volume, depending on the individual's position. Gas is added to the bladder when a ray-finned fish swims down; gas is removed when the fish swims up. In this way, ray-finned fishes maintain neutral buoyancy in water of various depths and thus various pressures. ● You should be able to indicate the origin of rayed fins and the swim bladder on Figure 34.22 on page 788.

The actinopterygians are the most successful vertebrate lineage based on number of species, duration in the fossil record, and extent of habitats occupied. Almost 27 000 species of ray-finned fishes have been identified thus far. In traditional classifications, Actinopterygii is considered a class.

The most important major lineage of ray-finned fishes is the Teleostei. About 96 percent of all living fish species, including familiar groups like the tuna, trout, cod, and goldfish, are teleosts (**Figure 34.27**).

Holocentrus rufus

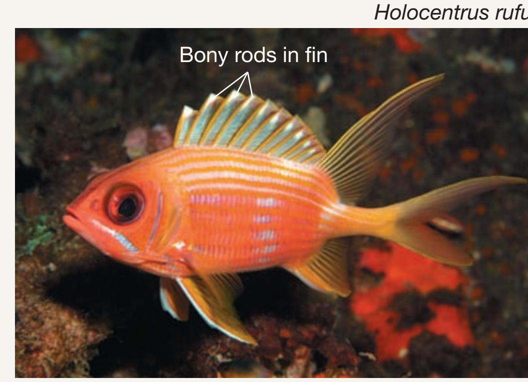


FIGURE 34.27 Teleosts Are Ray-Finned Fishes That Have a Flexible Tail.

Feeding Teleosts can suck food toward their mouths, grasp it with their protrusible jaws, and then process it with teeth on their jaws and with pharyngeal jaws in their throat. The size and shape of the mouth, the jaw teeth, and the pharyngeal jaw teeth all correlate with the type of food consumed. For example, most predatory teleosts have long, spear-shaped jaws armed with spiky teeth, as well as bladelike teeth on their pharyngeal jaws. Besides being major predators, ray-finned fishes are the most important large herbivores in both marine and freshwater environments.

continued

Chordata > Vertebrata> Actinopterygii (Ray-Finned Fishes) *continued*

Movement Ray-finned fishes swim by alternately contracting muscles on the left and right sides of their bodies from head to tail, resulting in rapid, side-to-side undulations. Their bodies are streamlined to reduce drag in water. Teleosts have a flexible, symmetrical tail, which reduces the need to use their pectoral (side) fins as steering and stabilizing devices during rapid swimming.

Reproduction Most ray-finned fish species rely on external fertilization and are oviparous; some species have internal fertilization with external development; still others have internal fertilization and are viviparous. Although it is common for fish eggs to be released in the water and left to develop on their own, parental care occurs in some species. Parents may carry fertilized eggs on their fins, in their mouth, or in specialized pouches to guard them until the eggs hatch. In freshwater teleosts, offspring develop directly; but marine species have larva that are very different from adult forms. As they develop, marine fish larvae undergo a metamorphosis to the juvenile form, which then grows into an adult.

Chordata > Vertebrata > Sarcopterygii > Actinistia (Coelacanths) and Dipnoi (Lungfish)

Although coelacanths (pronounced *SEEL-uh-kanths*) and lungfish represent independent lineages, they are sometimes grouped together and called **lobe-finned fishes**. Lobe-finned fishes are common and diverse in the fossil record in the Devonian period, about 400 million years ago, but only eight species are living today. They are important, however, because they represent a crucial evolutionary link between the ray-finned fishes and the tetrapods. Instead of having fins supported by rays of bone, their fins are fleshy lobes supported by a linear—not radial—array of bones and muscles, similar to those observed in the limbs of tetrapods (**Figure 34.28**). You should be able to indicate the origin of a linear array of fin bones on Figure 34.22 on page 788.

Coelacanths are marine and occupy habitats 150–700 m below the surface. In contrast, lungfish live in shallow, freshwater ponds and rivers (see Figure 34.11 on page 782). As their name implies, lungfish have lungs and breathe air when oxygen levels in their habitats drop. Some species burrow in mud and enter a quiescent, sleeplike state when their habitat dries up during each year's dry season.

Feeding Coelacanths prey on fish. Lungfish are **omnivorous** ("all-eating"), meaning that they eat algae and plant material as well as animals.

Movement Coelacanths swim by waving their pectoral and pelvic ("hip") fins in the same sequence that tetrapods use in walking with their limbs. Lungfish swim by waving their bodies, and they can use their fins to walk along pond bottoms.

Reproduction Sexual reproduction is the rule, with fertilization internal in coelacanths and external in lungfish. Coelacanths are ovoviviparous; lungfish lay eggs. Lungfish eggs hatch into larvae that resemble juvenile salamanders.

Latimeria chalumnae

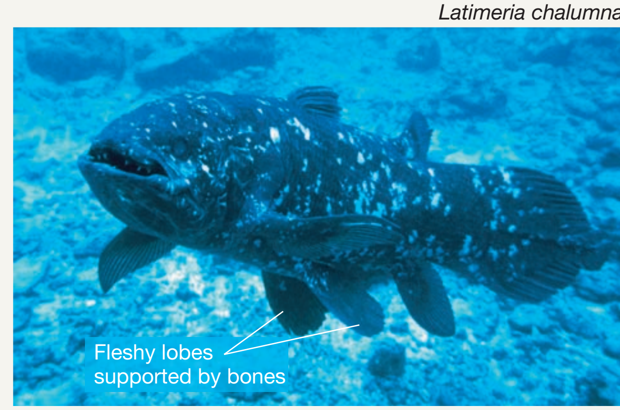


FIGURE 34.28 Coelacanths Are Lobe-Finned Fishes.

Chordata > Vertebrata > Amphibia (Frogs, Salamanders, Caecilians)

The 5500 species of **amphibians** living today form three distinct clades traditionally termed orders: (1) frogs and toads, (2) salamanders, and (3) caecilians (pronounced *suh-SILL-ee-uns*). Amphibians are found throughout the world and occupy ponds, lakes, or moist terrestrial environments (**Figure 34.29a**). Translated literally, their name means "both-sides-living." The name is appropriate because adults of most species of amphibians feed on land but lay their eggs in water. In many species of amphibians, gas exchange occurs exclusively or in part across their moist, mucus-covered skin. You should be able to indicate the origin of "skin-breathing" on Figure 34.22 on page 788.

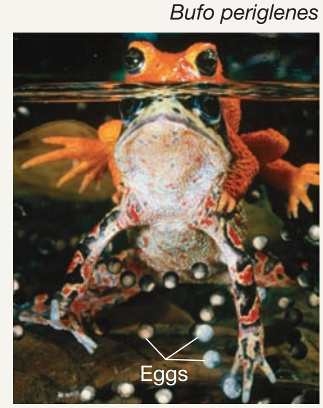
Feeding Adult amphibians are carnivores. Most frogs are sit-and-wait predators that use their long, extensible tongues to capture passing prey. Salamanders also have an extensible tongue, which some species use in feeding. Terrestrial caecilians prey on earthworms and other soil-dwelling animals; aquatic forms eat vertebrates and small fish.

Movement Most amphibians have four well-developed limbs. In water, frogs and toads move by kicking their hind legs to swim; on land they kick their hind legs out to jump or hop. Salamanders walk on land; in water they undulate their bodies to swim. Caecilians lack limbs and eyes; terrestrial forms burrow in moist soils (**Figure 34.29b**).

Reproduction Frogs are oviparous and have external fertilization, but salamanders and caecilians have internal fertilization. Most salamanders are oviparous, but many caecilians are viviparous. In some species of frogs, parents may guard or even carry eggs. In many frogs, young develop in the water and suspension feed on plant or algal material. Salamander larvae are carnivorous. Later the larvae undergo a dramatic metamorphosis into land-dwelling adults. For example, the fishlike tadpoles of frogs and toads develop limbs, and their gills are replaced with lungs.

(a) Frogs and other amphibians lay their eggs in water.

Bufo periglenes



(b) Caecilians are legless amphibians.

Ichthyophis kohtaoensis

FIGURE 34.29 Amphibians Are the Most Ancient Tetrapods.

Mammalia (Mammals)

Mammals are easily recognized by the presence of hair or fur, which serves to insulate the body. Like birds, mammals are endotherms that maintain high body temperatures by oxidizing large amounts of food and generating large amounts of heat. Instead of insulating themselves with feathers, though, mammals retain heat because the body surface is covered with layers of hair or fur. Endothermy evolved independently in birds and mammals. In both groups, endothermy is thought to be an adaptation that enables individuals to maintain high levels of activity— particularly at night or during cold weather.

In addition to being endothermic and having fur, mammals have **mammary glands**—a unique structure that makes lactation possible. The evolution of mammary glands gave mammals the ability to provide their young with particularly extensive parental care. Mammals are also the only vertebrates with facial muscles and lips and the only vertebrates that have a lower jaw formed from a single bone. In traditional classifications, Mammalia is designated as a class (**Figure 34.30**).

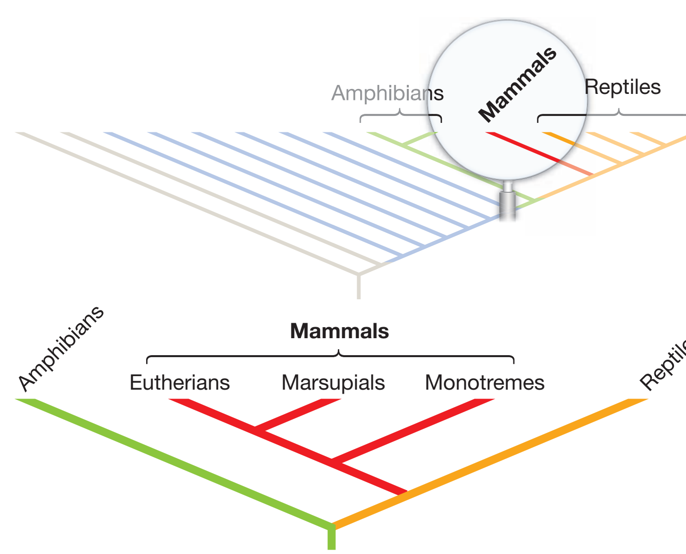


FIGURE 34.30 Mammals Are a Monophyletic Group.

Mammals evolved when dinosaurs and other reptiles were the dominant large herbivores and predators in terrestrial and aquatic environments. The earliest mammals in the fossil record appear about 195 million years ago; most were small animals that were probably active only at night. Many of the 4800 species of mammals living today have good nocturnal vision and a strong sense of smell, as their ancestors presumably did. The adaptive radiation that gave rise to today's diversity of mammals did not take place until after the dinosaurs went extinct about 65 million years ago. After the dinosaurs were gone, the mammals diversified into lineages of small and large herbivores, small and large predators, or marine hunters—ecological roles that had once been filled by dinosaurs and the ocean-dwelling, extinct reptiles called mosasaurs.

Mammalia > Monotremata (Platypuses, Echidnas)

The **monotremes** are the most ancient lineage of mammals living today, and they are found only in Australia and New Zealand. They lay eggs and have metabolic rates—meaning a rate of using oxygen and oxidizing sugars for energy—that are lower than other mammals. Three species exist: one species of platypus and two species of echidna. ● You should be able to indicate the origin of fur and lactation on Figure 34.30.

Feeding Monotremes have a leathery beak or bill. The platypus feeds on insect larvae, molluscs, and other small animals in streams (**Figure 34.31a**). Echidnas feed on ants, termites, and earthworms (**Figure 34.31b**).

Movement Platypuses swim with the aid of their webbed feet. Echidnas walk on their four legs.

Reproduction Platypuses lay their eggs in a burrow, while echidnas keep their eggs in a pouch on their belly. The young hatch quickly, and the mother must continue keeping them warm and dry for another four months.

(a) Platypus

Ornithorhynchus anatinus

(b) Echidna

Tachyglossus aculeatus

FIGURE 34.31 Platypuses and Echidnas Are Egg-Laying Mammals.

Mammalia > Marsupiala (Marsupials)

The 275 known species of **marsupials** live in the Australian region and the Americas (**Figure 34.32**) and include the familiar opossums, kangaroos, wallabies, and koala. Although females have a placenta that nourishes embryos during development, the young are born after a short embryonic period and are poorly developed. They crawl from the opening of the female's reproductive tract to the female's nipples, where they suck milk. They stay attached to their mother until they grow large enough to move independently. ● You should be able to indicate the origin of the placenta and viviparity—traits that are also found in Eutherian mammals—on Figure 34.30.

Feeding Marsupials are herbivores, omnivores, or carnivores. In many cases, convergent evolution has resulted in marsupials that are extremely similar to placental species in overall morphology and way of life. For example, a recently extinct marsupial called the Tasmanian wolf was a long-legged, social hunter similar to the timber wolves of North America and northern Eurasia. A species of marsupial native to Australia specializes in eating ants and looks and acts much like the South American anteater, which is not a marsupial.

Movement Marsupials move by crawling, gliding, walking, running, or hopping.

Reproduction Marsupial young spend more time developing while attached to their mother's nipple than they do inside her body being fed via the placenta.

Didelphis virginiana

FIGURE 34.32 Marsupials Give Birth after a Short Embryonic Period. Opossums are the only marsupials in North America.

Mammalia > Eutheria (Placental Mammals)

The approximately 4300 species of **placental mammals**, **eutherians**, are distributed worldwide. They are far and away the most species-rich and morphologically diverse group of mammals.

Biologists group placental mammals into 18 lineages called orders. The six most species-rich orders are the rodents (rats, mice, squirrels; 1814 species), bats (986 species), insectivores (hedgehogs, moles, shrews; 390 species), artiodactyls (pigs, hippos, whales, deer, sheep, cattle; 293 species), carnivores (dogs, bears, cats, weasels, seals; 274 species), and primates (lemurs, monkeys, apes, humans; 235 species).

Feeding The size and structure of the teeth correlate closely with the diet of placental mammals. Herbivores have large, flat teeth for crushing leaves and other coarse plant material; predators have sharp teeth that are efficient at biting and tearing flesh. Omnivores, such as humans, usually have several distinct types of teeth. The structure of the digestive tract also correlates with the placental mammals' diet. In some plant-eaters, for example, the stomach hosts unicellular organisms that digest cellulose and other complex polysaccharides.

Movement In placental mammals, the structure of the limb correlates closely with the type of movement performed. Eutherians fly, glide, run, walk, swim, burrow, or swing from trees (**Figure 34.33**). Limbs are reduced or lost in aquatic groups such as whales and dolphins, which swim by undulating their bodies.

Reproduction Eutherians have internal fertilization and are viviparous. An extensive placenta develops from a combination of maternal and fetal tissues; and at birth, young are much better developed than in marsupials—some are able to walk or run minutes after emerging from the mother. You should be able to indicate the origin of delayed birth (extended development prior to birth) on Figure 34.30. All eutherians feed their offspring milk until the young have grown large enough to process solid food. A prolonged period of parental care, extending beyond the nursing stage, is common as offspring learn how to escape predators and find food on their own.

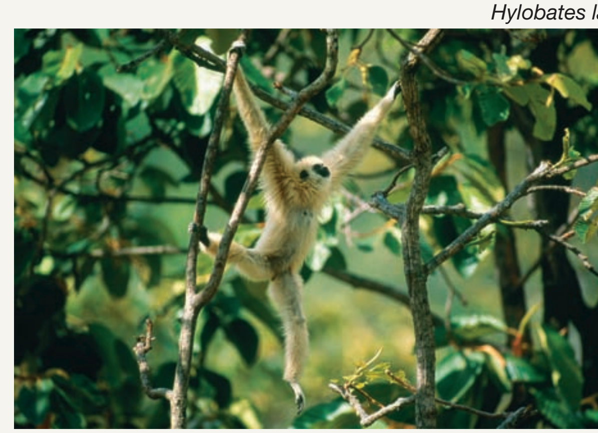


FIGURE 34.33 Eutherians Are the Most Species-Rich and Diverse Group of Mammals.

Reptilia (Turtles, Snakes and Lizards, Crocodiles, Birds)

The **reptiles** are a monophyletic group and represent one of the two major living lineages of amniotes—the other lineage consists of the extinct mammal-like reptiles and today's mammals. The major feature distinguishing the reptilian and mammalian lineages is the number and placement of openings in the side of the skull. Jaw muscles that make possible sophisticated biting and chewing movements pass through these openings and attach to bones on the upper part of the skull.

Several features adapt reptiles for life on land. Their skin is made watertight by a layer of scales made of the protein keratin, which is also a major component of mammalian hair. Reptiles breathe air through well-developed lungs and lay shelled, amniotic eggs that resist drying out. In turtles, the egg has a leathery shell; in other reptiles, the shell is made of stiff calcium carbonate. Fertilization is internal because the sperm and egg have to meet and form the zygote before the amniotic membrane and shell form. If fertilization were external, sperm would have to pass through the shell and amnion to reach the egg cell.

The reptiles include the dinosaurs, pterosaurs (flying reptiles), mosasaurs (marine reptiles), and other extinct lineages that flourished from about 250 million years ago until the mass extinction at the end of the Cretaceous period, 65 million years ago. Today the Reptilia are represented by four major lineages, traditionally recognized as subclasses: (1) turtles, (2) snakes and lizards, (3) crocodiles and alligators, and (4) birds (**Figure 34.34**). Except for birds, all of these groups are **ectothermic** ("outside-heated")—meaning that individuals do not use internally generated heat to regulate their body temperature. It would be a mistake, however, to conclude that reptiles other than birds do not regulate their body temperature closely. Reptiles bask in sunlight, seek shade, and perform other behaviours to keep their body temperature at a preferred level.

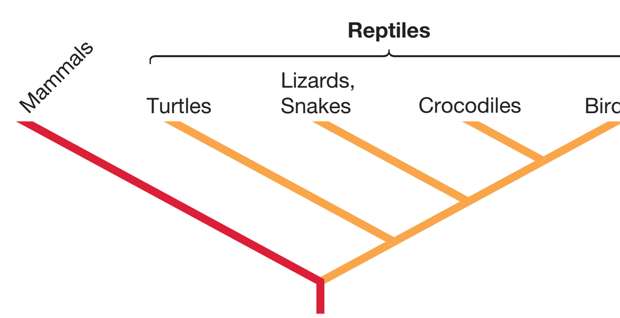


FIGURE 34.34 Reptiles Are a Monophyletic Group.

CANADIAN **ISSUES** 34.1

Alberta During the Mesozoic Era

Dinosaur Provincial Park

The approach to Alberta's Dinosaur Provincial Park is over a broad expanse of dry, rolling grasslands (**Figure A**). As visitors enter the park, the land drops away, eroded by wind and water to reveal Canada's largest badlands. The badlands, formed from Cretaceous period sandstone, expose one of the world's richest sources of dinosaur fossils. This eerie landscape makes it easy to imagine the lost world of 72 million years ago, when this area was a subtropical coastal floodplain on the western margin of a warm inland sea. With lush forests, meandering rivers, and cypress swamps, conditions were ideal for the fossilization of the remains of dinosaurs and the organisms that shared their world.

First Nations people were the first to find dinosaur fossils in Alberta, calling the fossils "the grandfather of the buffalo." Over the last century, dinosaur expeditions and excavations have unearthed millions of bones from almost 40 species of dinosaurs, a significant percentage of the total number of dinosaur species identified worldwide. Dinosaur Provincial Park alone has yielded 150 complete dinosaur skeletons, plus 20 bonebeds with dense concentrations of bones and bone fragments. The park, named a UNESCO World Heritage Site in 1979, was the first paleontological site in the world to be given this honour. In 1985, the Alberta government opened the Royal Tyrell Museum of Palaeontology, which displays these fossils to over 400 000 visitors a year.

Figure A *The Red Deer River runs through Dinosaur Provincial Park, near Brooks, Alberta.*

Dr. Philip J. Currie

Phil Currie's interest in dinosaurs was sparked when he tipped a plastic one out of a cereal box at age six; by age 11, he had decided to become a paleontologist. Currie (**Figure B**) was named curator of paleontology at the Provincial Museum of Alberta in 1976 and was instrumental in founding the Royal Tyrrell Museum of Palaeontology. He has tracked dinosaurs in the deserts of Mongolia, through the badlands of Argentina, on the margins of the Arctic Ocean on Ellesmere Island, Nunavut, and in Dinosaur Provincial Park.

Currie has published articles on a wide range of topics. With Chinese colleagues, he has identified and described feathers on the forearms and tails of non-flying dinosaurs. A feather is far too complex a structure to have arisen multiple times, and this finding confirms that birds are living dinosaurs. He and his collaborators have described the powerful bite of *Tyrannosaurus rex* and modelled how a sauropod dinosaur lashed its thin, tapering tail like a bullwhip, creating the deafening crack of a sonic boom as it broke the sound barrier. He has worked out life tables and survivorship curves for the tyrannosaurid *Albertosaurus*, as described in Canadian Research 52.1 on page 1232. Currie is now a professor at the University of Alberta, where he is working to understand the paleoecology of the late Cretaceous period in Alberta by studying the fossils of Dinosaur Provincial Park. Currie has never lost his enthusiasm for finding and understanding dinosaurs. "It's the nature of the game," he says. "Paleontology doesn't let you lose interest or your excitement. It's like having a career of going out and finding buried treasure."

Reconstructing a Cretaceous World

Philip Currie points out that it is difficult to study paleobehaviour: the behaviour of extinct animals. Though speculative, inferences about dinosaur behaviour can be drawn from a number of lines of evidence. Dinosaur trackways provide information about the movement and interactions of dinosaurs, including their speed, the existence and organization of herds, and the possibility that they undertook seasonal migrations. Bonebeds or groups of fossils that are formed entirely or mainly by a single species suggest that the animals that died together lived as a social herd. Communal nesting sites provide evidence of social interaction and parental care. Morphological features and evidence of injury or disease in dinosaur fossils are also informative, especially when combined with analysis of similar features in living animals.

Dinosaur Provincial Park contains 20 bonebeds with dense aggregations of thousands of fossilized bones and bone fragments

Figure B *Dr. Philip J. Currie.*

continued

CANADIAN **ISSUES** 34.1 *(continued)*

of horned dinosaurs, or ceratopsians. Each bonebed contains juvenile, subadult, and adult dinosaurs, suggesting that all of them died together. The most likely scenario to explain the bonebeds is a mass drowning. Perhaps a herd of ceratopsians drowned on a flooded plain, following heavy rains. Perhaps a herd died during migration, as the dinosaurs tried to cross a flooded river. **Figure C** illustrates this scenario, with a herd of migrating *Centrosaurus* fording a river. As water receded from the floodplain or river, the dinosaur carcasses were carried along and deposited along curves in river channels. Tyrannosaur teeth are scattered in the bonebeds, suggesting scavenging of the dead bodies.

Ceratopsian bonebeds suggest that *Centrosaurus* and other horned dinosaurs interacted socially in large herds. Perhaps they nested in small groups on the coastline, migrating inland to the Dinosaur Provincial Park area in large herds to reduce their predation risk. What other evidence supports the hypothesis that ceratopsian dinosaurs lived in large herds?

Ceratopsians are large quadrupedal herbivores. Both sexes have prominent species-specific horns and frills. The functions of similar structures in modern animal populations may provide clues about their role in ceratopsian behaviour. Cranial features like horns and frills without sexual dimorphism are characteristic of large, non-territorial, mixed-sex herds with an established status hierarchy. In such herds, large mature males dominate young males, inhibiting their reproduction until they are large enough to compete for access to females. *Centrosaurus* fossils show evidence of delayed sexual maturity in males, typical of vertebrates who live in such herds. Herding offers considerable protection against predators, especially for juvenile and baby ceratopsians. Herd animals can devote less time and effort to predator vigilance, allowing them more time for feeding. When females have well-developed horns, they are able to resist sexual advances from juvenile males, can compete with males for access to food, and are less likely to be singled out for attack by predators.

Were tyrannosaurs also gregarious? A number of lines of evidence suggest that they were. Fossil assemblages from several tyrannosaur species, including *Tyrannosaurus rex*, have been found. The assemblages include adult, juvenile, and baby tyrannosaurs that likely lived together before they died. Tyrannosaurs did not reach sexual maturity until they were teenagers, and juvenile tyrannosaurs were doubtless faster and more agile than their parents. Currie suggests that tyrannosaur groups may have hunted cooperatively, with speedy juveniles driving prey toward the massive and powerful adults. Their preferred prey was the duckbilled hadrosaur, based on the high numbers of hadrosaur bones with tyrannosaur toothmarks.

Tyrannosaur interactions were characterized by considerable intraspecific aggression: Fully 44 percent of the intact tyrannosaur skulls prepared at the Royal Tyrell Museum of Palaeontology have healed bite marks. Traumatic injuries to tyrannosaur skulls include single or multiple tooth punctures and damaged teeth with drag marks from the serrated teeth of other tyrannosaurs. One tyrannosaur had a broken-off tooth embedded in its lower jaw. Aggressive headbiting is well known in many living and extinct vertebrates, from sharks to sabertoothed tigers to crocodilians.

Figure D shows the facial injuries suffered by a young *Gorgosaurus libratus* from Dinosaur Provincial Park, including a possible jaw fracture caused by a bite on the right-hand side of the lower jaw. A broken tooth in the upper jaw lines up with the fracture site in the lower jaw. The dinosaur would also have suffered muscle and skin damage at the site of the injury. The injury was healing when the tyrannosaur died, with a new tooth emerging at the site of the broken one. However, the wounds were only partially healed, suggesting that the young dinosaur may have died as a result of his injuries, which may have become infected or prevented him from eating effectively.

What led to aggression between tyrannosaurs? These large carnivores likely lived in social groups, and they may have fought over mating opportunities, for access to a kill, or to establish status within a social group. Young tyrannosaurs were particularly vulnerable to intraspecific attack.

Sixty-five million years ago, an asteroid strike ended the Cretaceous period. The fossils of Dinosaur Provincial Park provide the best evidence of the late Cretaceous, when the last of the great dinosaurs dominated terrestrial communities.

Figure C *A* Centrosaurus *herd fords a river.*

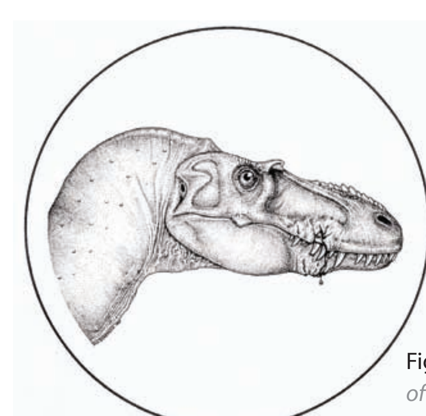


Figure D *Reconstruction of facial injuries to a young* Gorgosaurus libratus.

Reptilia > Testudinia (Turtles)

The 300 known species of turtles inhabit freshwater, marine, and terrestrial environments throughout the world. The testudines are distinguished by a shell composed of bony plates, covered with a material similar in composition to human fingernails, that fuse to the vertebrae and ribs (**Figure 34.35**). You should be able to indicate the origin of the turtle shell on Figure 34.34. The turtles' skulls are highly modified versions of the skulls of other reptiles. Turtles lack teeth, but their jawbone and lower skull form a bony beak.

Feeding Turtles are either carnivorous—feeding on whatever animals they can capture and swallow—or herbivorous. They may also scavenge dead material. Most marine turtles are carnivorous. Leatherback turtles, for example, feed primarily on jellyfish, and they are only mildly affected by the jellyfish's stinging cnidocytes (see Chapter 32). In contrast, species in the lineage of terrestrial turtles called the tortoises are plant-eaters.

Movement Turtles swim, walk, or burrow. Aquatic species usually have feet that are modified to function as flippers.

Reproduction All turtles are oviparous. Other than digging a nest prior to depositing eggs, parental care is lacking. The sex of a baby turtle is often not determined by sex chromosomes. Instead, in many species gender is determined by the temperature at which the egg develops. High temperatures produce mostly males, while low temperatures produce mostly females.

Testudo pardalis

FIGURE 34.35 Turtles Have a Shell Consisting of Bony Plates.

Reptilia > Lepidosauria (Lizards, Snakes)

Most lizards and snakes are small reptiles with elongated bodies and scaly skin. Most lizards have well-developed jointed legs, but snakes are limbless (**Figure 34.36**). The hypothesis that snakes evolved from limbed ancestors is partially supported by the presence of vestigial hip and leg bones in boas and pythons. There are about 7000 species of lizards and snakes alive now. You should be able to indicate the origin of scaly skin on Figure 34.34 on page 797.

Feeding Small lizards prey on insects. Although most of the larger lizard species are herbivores, the 3-metre-long monitor lizard from the island of Komodo is a predator that kills and eats deer. Snakes are carnivores; some subdue their prey by injecting poison through modified teeth called fangs. Snakes prey primarily on small mammals, amphibians, and invertebrates, which they swallow whole—usually headfirst.

Movement Lizards crawl or run on their four limbs. Snakes and limbless lizards burrow through soil, crawl over the ground, or climb trees by undulating their bodies.

Reproduction Although most lizards and snakes lay eggs, many are oviviviparous. Most species reproduce sexually, but asexual reproduction, via the production of eggs by mitosis, is known to occur in six groups of lizards and one snake lineage.

Morelia viridis

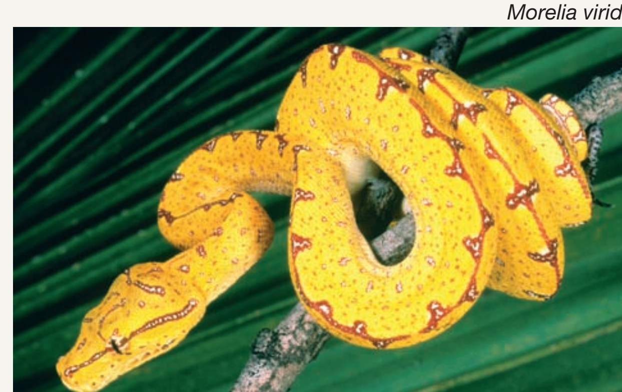


FIGURE 34.36 Snakes Are Limbless Predators.

Reptilia > Crocodilia (Crocodiles, Alligators)

Only 24 species of crocodiles and alligators are known. Most are tropical and live in freshwater or marine environments. They have eyes located on the top of their head and nostrils located at the top of their long snout—adaptations that allow them to sit semi-submerged in water for long periods of time (**Figure 34.37**).

Feeding Crocodilians are predators. Their jaws are filled with conical teeth that are continually replaced as they fall out during feeding. Their usual method of killing small prey is by biting through the body wall. Large prey are usually subdued by drowning. Crocodilians eat amphibians, turtles, fish, birds, and mammals.

Movement Crocodiles and alligators walk or gallop on land. In water they swim with the aid of their large, muscular tails.

Reproduction Although crocodilians are oviparous, parental care is extensive. Eggs are laid in earth-covered nests that are guarded by the parents. When young inside the eggs begin to vocalize, parents dig them up and carry the newly hatched young inside their mouth to nearby water. Crocodilian young can hunt when newly hatched but stay near their mother for up to three years. ● You should be able to indicate the origin of extensive parental care—which also occurs in birds (and dinosaurs)—on Figure 34.34 on page 797.

Alligator mississippiensis

FIGURE 34.37 Alligators Are Adapted for Aquatic Life.

Reptilia > Aves (Birds)

The fossil record provides conclusive evidence that birds descended from a lineage of dinosaurs that had a unique trait: **feathers**. In dinosaurs, feathers are hypothesized to have functioned as insulation and in courtship or aggressive displays. In birds, feathers insulate and are used for display but also furnish the lift, power, and steering required for flight. Birds have many other adaptations that make flight possible, including large breast muscles used to flap the wings. Bird bodies are lightweight because they have a reduced number of bones and organs and because their hollow bones are filled with air sacs linked to the lungs. Instead of teeth, birds have a horny beak. They are endotherms (“within-heating”), meaning that they have a high metabolic rate and use the heat produced, along with the insulation provided by feathers, to maintain a constant body temperature. The 9100 bird species alive today occupy virtually every habitat, including the open ocean (**Figure 34.38**). ● You should be able to indicate the origin of feathers, endothermy, and flight on Figure 34.34 on page 797.

Feeding Plant-eating birds usually feed on nectar or seeds. Most birds are omnivores, although many are predators that capture insects, small mammals, fish, other birds, lizards, molluscs, or crustaceans. The size and shape of a bird’s beak correlate closely with its diet. For example, predatory species such as falcons have sharp, hook-shaped beaks; finches and other seedeaters have short, stocky bills that can crack seeds and nuts; fish-eating species such as the great blue heron have spear-shaped beaks.

Movement Although flightlessness has evolved repeatedly during the evolution of birds, almost all species can fly. The size and shape of birds’ wings correlate closely with the type of flying they do. Birds that glide or hover have long, thin wings; species that specialize in explosive takeoffs and short flights have short, stocky wings. Many seabirds are efficient swimmers, using their webbed feet to paddle or flapping their wings to “fly” under water. Ground-dwelling birds such as ostrich and pheasants can run long distances at high speed.

Reproduction Birds are oviparous but provide extensive parental care. In most species, one or both parents build a nest and incubate the eggs. After the eggs hatch, parents feed offspring until they are large enough to fly and find food on their own.

Diomedea melanophris

FIGURE 34.38 Birds Are Feathered Descendants of Dinosaurs.

34.6 Key Lineages: The Hominin Radiation

Although humans occupy a tiny twig on the tree of life, there has been a tremendous amount of research on human origins. This section introduces the lineage of mammals called the Primates, the fossil record of human ancestors, and data on the relationships among human populations living today.

The Primates

The lineage called Primates consists of two main groups: prosimians and anthropoids. The **prosimians** ("before-monkeys") consist of the lemurs, found in Madagascar, and the tarsiers, pottos, and lorises of Africa and South Asia. Most prosimians live in trees and are active at night (**Figure 34.39a**). The Anthropoidea or **anthropoids** ("human-like") include the New World monkeys found in Central and South America, the Old World monkeys that live in Africa and tropical regions of Asia, the gibbons of the Asian tropics, and the Hominidae, or **great apes**—orangutans, gorillas, chimpanzees, and humans (**Figure 34.39b**). The phylogenetic tree in **Figure 34.40** shows the evolutionary relationships among these groups.

Primates are distinguished by having eyes located on the front of the face. Eyes that look forward provide better depth perception than do eyes on the sides of the face. Primates also tend to have hands and feet that are efficient at grasping, flattened nails instead of claws on the fingers and toes, brains that are large relative to overall body size, complex social behaviour, and extensive parental care of offspring.

The lineage in Figure 34.40 that is composed of the great apes, including humans, is known as the Hominidae or **hominids**. From extensive comparisons of DNA sequence data, it is now clear that humans are most closely related to the chimpanzees and that our next nearest living relatives are the gorillas.

Compared with most types of primates, the great apes are relatively large bodied and have long arms, short legs, and no tail. Although all of the great ape species except for the orangutans live primarily on the ground, they have distinct ways of walking. When orangutans do come to the ground, they occasionally walk with their knuckles pressed to the ground. More commonly, though, they fist-walk—that is, they walk with the backs of their hands pressed to the ground. Gorillas and chimps, in contrast, only knuckle-walk. They also occasionally rise up on two legs—usually in the context of displaying aggression. Humans are the only great ape that is fully **bipedal** ("two-footed")—meaning they walk upright on two legs. Bipedalism is, in fact, the shared derived character that defines the group called hominins. The Homininae, or **hominins**, are a monophyletic group comprising *Homo sapiens* and more than a dozen extinct, bipedal relatives.

Fossil Humans

According to the fossil record, the common ancestor of chimps and humans lived in Africa about 7 million years ago. As a group, all the species on the branch leading to contemporary humans are considered hominins. The fossil record of hominins, though not nearly as complete as investigators would like, is rapidly improving. About 14 species have been found to date, and new fossils that inform the debate over the ancestry of humans are discovered every year. Although naming the hominin species and interpreting their characteristics remain intensely controversial, most researchers agree that they can be organized into four groups:

1. ***Australopithecus*** Four species of small apes called gracile australopithecines have been identified thus far

(a) Prosimians are small, tree-dwelling primates.

Loris tardigradus

(b) New World monkeys are anthropoids.

Ateles geoffroyi

FIGURE 34.39 There Are Two Main Lineages of Primates. (a) Prosimians live in Africa, Madagascar, and South Asia. **(b)** Anthropoids include Old World monkeys, New World monkeys, and great apes.

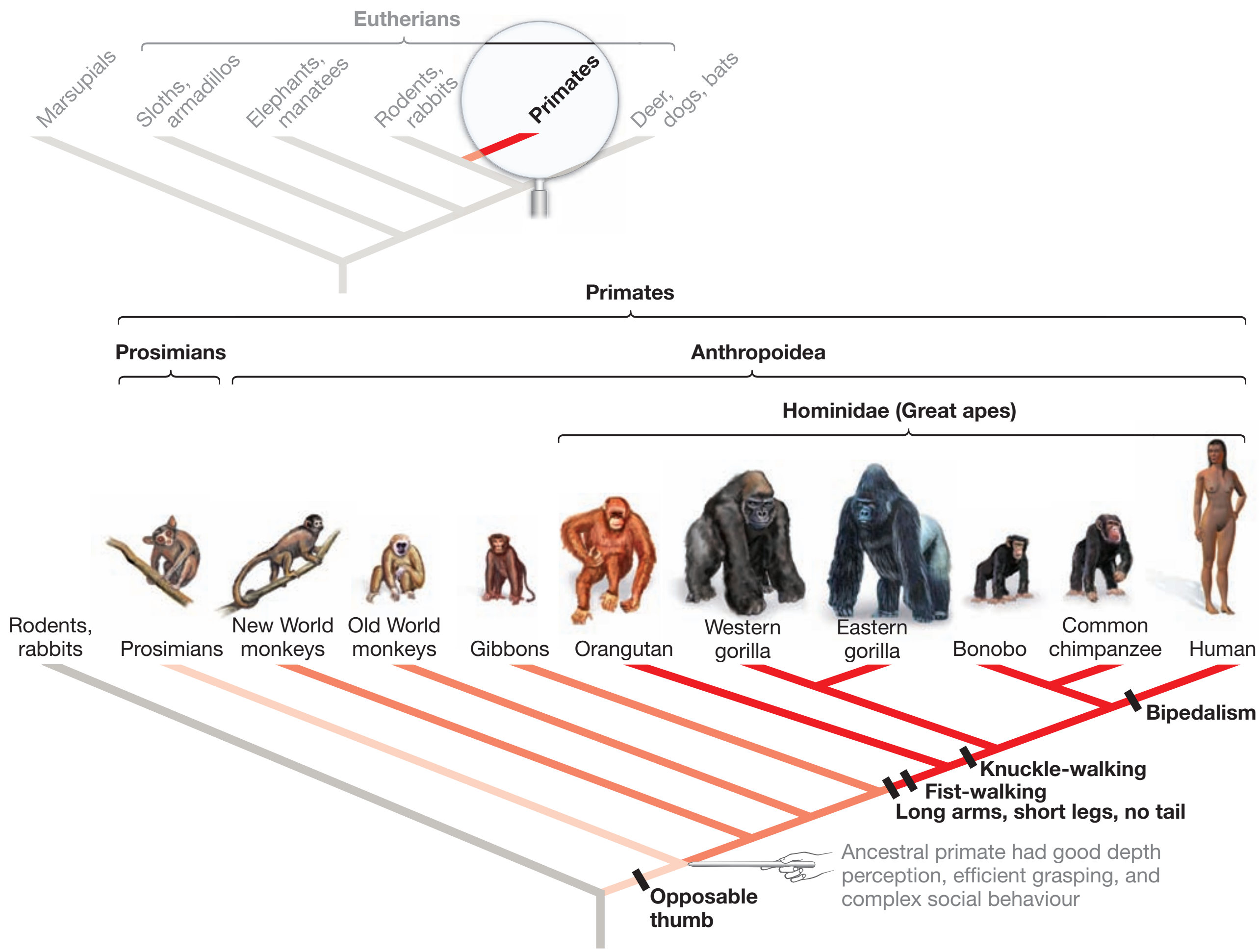


FIGURE 34.40 A Phylogeny of the Monkeys and Great Apes. Phylogenetic tree estimated from extensive DNA sequence data. According to the fossil record, humans and chimps shared a common ancestor 6 to 7 million years ago.

(**Figure 34.41a**). The adjective *gracile*, or "slender," is appropriate because these organisms were slightly built. Adult males were about 1.5 metres tall and weighed about 36 kg. The genus name *Australopithecus* ("southern ape") was inspired by the earliest specimens, which came from South Africa. Several lines of evidence support the hypothesis that the gracile australopithecines were bipedal. For example, the hole in the back of their skull where the spinal cord connects to the brain is oriented downward, just as it is in our species, *Homo sapiens*. In chimps, gorillas, and other vertebrates that walk on four feet, this hole is oriented backward.

2. ***Paranthropus*** Three species are grouped in the genus *Paranthropus* ("beside-human"). Like the gracile australopithecines, these robust australopithecines were bipedal. They were much stockier than the gracile forms, however—about the same height but an estimated 8–10 kilograms heavier on average. In addition, their skulls were much broader and more robust (**Figure 34.41b**). All three species had massive cheek teeth and jaws, very large cheekbones, and a sagittal crest—a flange of bone at the top of the skull. Because muscles that work the jaw attach to the sagittal crest and cheekbones, researchers conclude that these organisms had tremendous biting power and made their living by crushing large seeds or coarse plant materials. One species is nicknamed "nutcracker man." The name *Paranthropus* was inspired by the hypothesis that the three known species are a monophyletic group that was a side branch during human evolution—an independent lineage that went extinct.

3. **Early *Homo*** Species in the genus *Homo* are called **humans**. As **Figure 34.41c** shows, species in this genus have flatter and narrower faces, smaller jaws and teeth, and larger braincases than the earlier hominins do. (The **braincase** is the portion of the skull that encloses the brain.) The appearance of early members of the genus *Homo* in the fossil record coincides closely with the appearance of tools made of worked stone—most of which are interpreted as handheld choppers or knives. Although the fossil record does not exclude the possibility that *Paranthropus* made

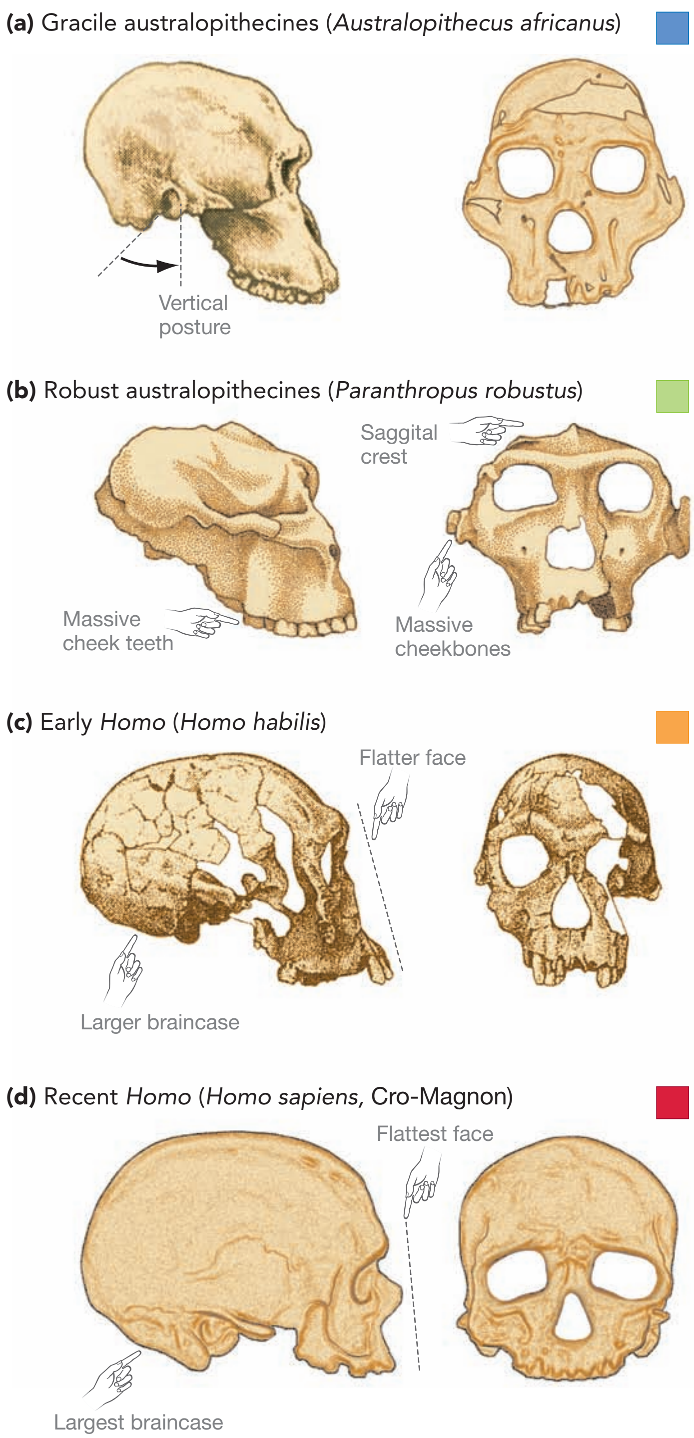


FIGURE 34.41 African Hominins Comprise Four Major Groups.

QUESTION The skulls are arranged as they appear in the fossil record, from most ancient to most recent—(a) to (d). How did the forehead and brow ridge of hominins change through time?

tools, many researchers favour the hypothesis that extensive toolmaking was a diagnostic trait of early *Homo*.

4. **Recent *Homo*** The recent species of *Homo* date from 1.2 million years ago to the present. As **Figure 34.41d** shows, these species have even flatter faces, smaller teeth, and larger braincases than the early *Homo* species do. The 30 000-year-old fossil in the figure, for example, is from a population of *Homo sapiens* (our species) called the **Cro-Magnons**. The Cro-Magnons were accomplished painters and sculptors who buried their dead in carefully prepared graves. There is also evidence that another species, the **Neanderthal** people (*Homo neanderthalensis*) made art and buried their dead in a ceremonial fashion. Perhaps the most striking recent *Homo*, though, is *H. floresiensis*. This species has been found only on the island of Flores in Indonesia, which was also home to a species of dwarfed elephants. *H. floresiensis* consisted of individuals that had braincases smaller than those of gracile australopithecines and were about a metre tall. Fossil finds suggest that the species inhabited the island from about 100 000 to 12 000 years before present and that dwarfed elephants were a major source of food.

Table 34.1 summarizes data on the geographic range, braincase volume, and body size of selected species within these four groups. **Figure 34.42** provides the time range of each species in the fossil record. Although researchers do not have a solid understanding of the phylogenetic relationships among the hominin species, several points are clear from the available data. First, the shared, derived character that defines the hominins is bipedalism. Second, several species from the lineage were present simultaneously during most of hominin evolution. For example, about 1.8 million years ago there may have been as many as five hominin species living in eastern and southern Africa. Because fossils from more than one species have been found in the same geographic location in rock strata of the same age, it is almost certain that different hominin species lived in physical contact. Finally, compared with the gracile and robust australopithecines and the great apes, species in the genus *Homo* have extremely large brains relative to their overall body size.

Why did humans evolve such gigantic brains? The leading hypothesis on this question is that early *Homo* began using symbolic spoken language along with initiating extensive tool use. The logic here is that increased toolmaking and language use triggered natural selection for the capacity to reason and communicate, which required a larger brain. To support this hypothesis, researchers point out that, relative to the brain areas of other hominins, the brain areas responsible for language were enlarged in the earliest *Homo* species. There is even stronger fossil evidence for extensive use of speech in *Homo neanderthalensis* and early *Homo sapiens*:

- The hyoid bone is a slender bone in the voice box of modern humans that holds muscles used in speech. In Neanderthals and early *Homo sapiens*, the hyoid is vastly different in size and shape from a chimpanzee's hyoid bone. Researchers recently found an intact hyoid bone associated with a 60 000-year-old Neanderthal individual and showed that it is virtually identical to the hyoid of modern humans.

TABLE **34.1** **Characteristics of Selected Hominins**

Species	Location of Fossils	Estimated Average Braincase Volume (cm^3)	Estimated Average Body Size (kg)	Associated with Stone Tools?
Australopithecus afarensis	Africa	450	36	no
A. africanus	Africa	450	36	no
Paranthropus boisei	Africa	510	44	no?
Homo habilis	Africa	550	34	yes
H. ergaster	Africa	850	58	yes
H. erectus	Africa, Asia	1000	57	yes
H. heidelbergensis	Africa, Europe	1200	62	yes
H. neanderthalensis	Middle East, Europe, Asia	1500	76	yes
H. floresiensis	Flores (Indonesia)	380	28	yes
H. sapiens	Middle East, Europe, Asia	1350	53	yes

- *Homo sapiens* colonized Australia by boat between 60 000 and 40 000 years ago. Researchers suggest that an expedition of that type could not be planned and carried out in the absence of symbolic speech.

To summarize, *Homo sapiens* is the sole survivor of an adaptive radiation that took place over the past 7 million years. From a common ancestor shared with chimpanzees, hominins evolved the ability to walk upright, make tools, and talk.

The Out-of-Africa Hypothesis

The first fossils of our own species, *Homo sapiens*, appear in African rocks that date to about 195 000 years ago. For some 130 000 years thereafter, the fossil record indicates that our species occupied Africa while *H. neanderthalensis* resided in Europe and the Middle East. Some evidence suggests that *H. erectus* may still have been present in Asia at that time. Then, in rocks dated between 60 000 and 30 000 years ago, *H. sapiens* fossils are found throughout Europe, Asia, Africa, and Australia. *H. erectus* had disappeared by this time, and *H. neanderthalensis* went extinct after coexisting with *H. sapiens* in Europe for perhaps a thousand years.

Phylogenies of *H. sapiens* estimated with DNA sequence data agree with the pattern in the fossil record. In phylogenetic trees that show the relationships among human populations living today, the first lineages to branch off lead to descendant populations that live in Africa today (**Figure 34.43**). Based on this observation, it is logical to infer that the ancestral population of modern humans also lived in Africa. The tree shows that lineages subsequently branched off to form three monophyletic groups. Because the populations within each of these clades live in a distinct area, the three lineages are thought to descend from three major waves of migration that occurred as a *Homo sapiens* population dispersed from east Africa to (1) north Africa, Europe, and central Asia, (2) northeast Asia and the Americas, and (3) southeast Asia and the South Pacific (**Figure 34.44**). To summarize, the data suggest that (1) modern humans originated in Africa; and (2) a population that left Africa split into three broad groups, which then spread throughout the world.

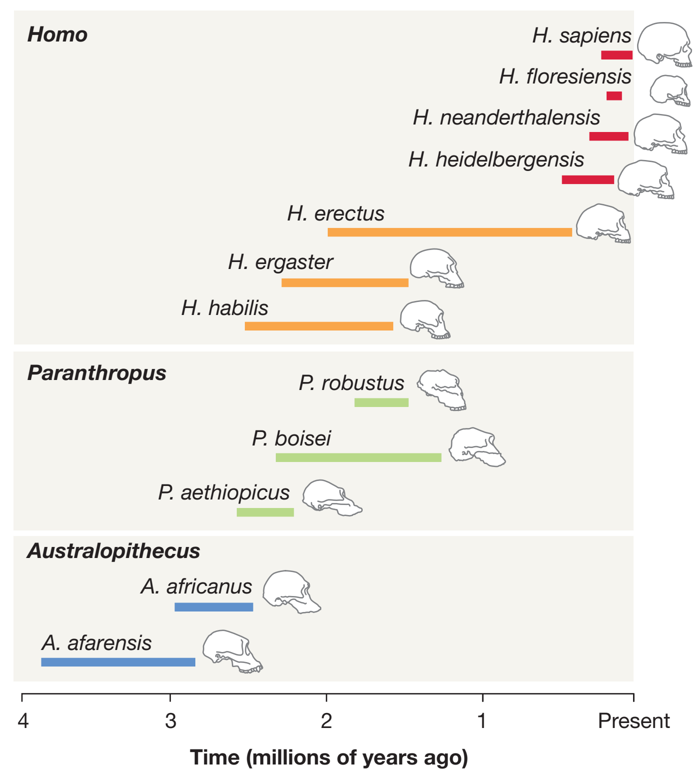


FIGURE 34.42 A Timeline of Human Evolution. Plot of the ages of selected fossil hominins.

QUESTION How many species of hominin existed 2.2 million years ago, 1.8 million years ago, and 100 000 years ago?

This scenario for the evolution of *H. sapiens* is called the **out-of-Africa hypothesis**. It contends that *H. sapiens* evolved independently of the earlier European and Asian species of *Homo*—meaning there was no interbreeding between *H. sapiens* and Neanderthals, *H. erectus*, or *H. floresiensis*. Stated another way, the out-of-Africa hypothesis proposes that *H. sapiens* evolved its distinctive traits in Africa and then dispersed throughout the world.

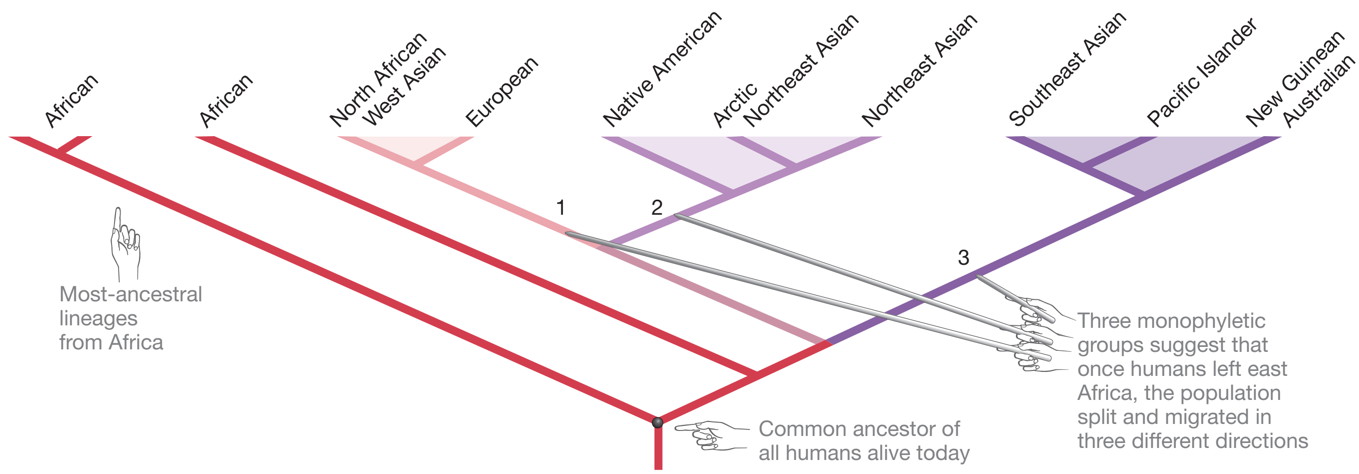


FIGURE 34.43 Phylogeny of Human Populations Living Today. Phylogeny of modern human populations, as estimated from DNA sequence data.

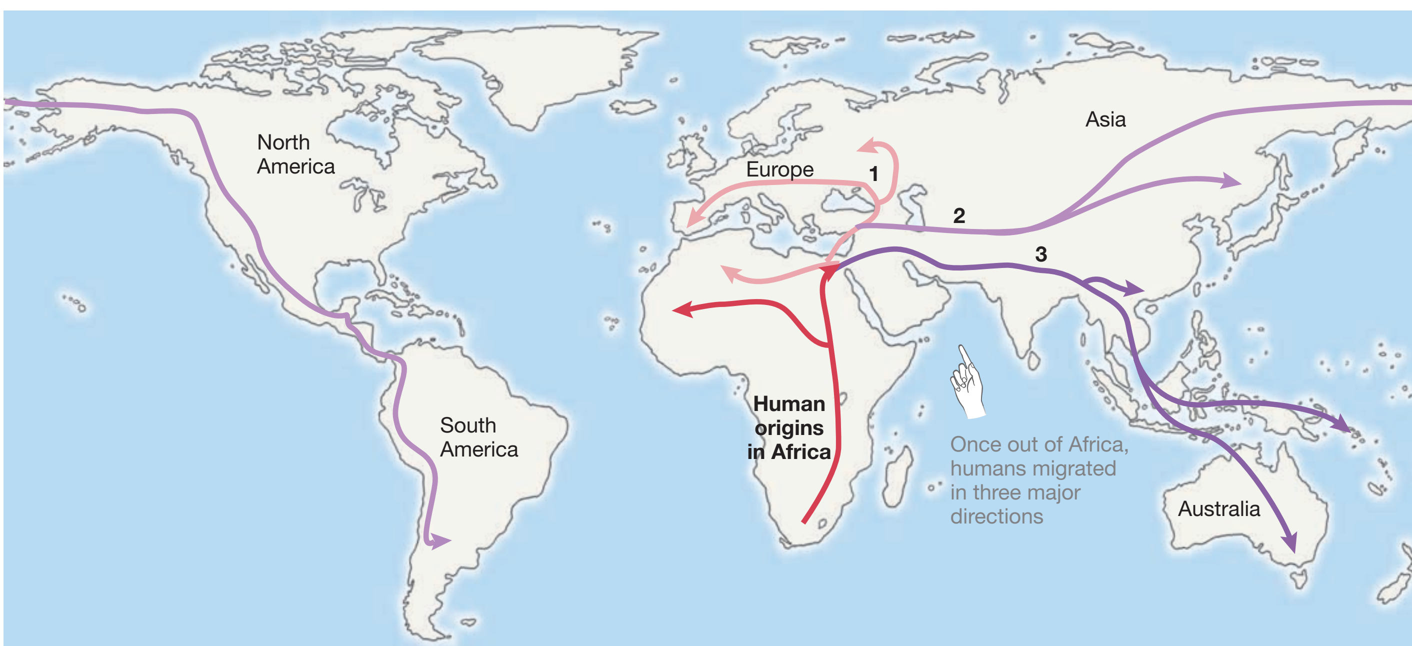


FIGURE 34.44 *Homo sapiens* Originated in Africa and Spread throughout the World. The phylogeny in Figure 34.43 supports the hypothesis that humans originated in Africa and spread out in three major migrations: to southeast Asia and the Pacific Islands, to Europe, and to northeast Asia and the New World.

Chapter Review

SUMMARY OF KEY CONCEPTS

- **The most species-rich deuterostome lineages are the echinoderms and the vertebrate groups called ray-finned fishes and tetrapods.**

  Echinoderms, ray-finned fishes, and tetrapods are also the most important large-bodied predators and herbivores in marine and terrestrial environments.

  You should be able to describe what food chains in aquatic and terrestrial environments would look like if echinoderms, ray-finned fishes, and tetrapods did not exist.

- **Echinoderms and vertebrates have unique body plans. Echinoderms are radially symmetric as adults and have a water vascular system. All vertebrates have a skull and an extensive endoskeleton made of cartilage or bone.**

  Echinoderm larvae are bilaterally symmetric but undergo a metamorphosis into radially symmetric adults. Their water vascular system is composed of fluid-filled tubes and chambers and extends from the body wall in projections called podia.

Podia can extend and retract in response to muscle contractions that move fluid inside the water vascular system.

Chordates are distinguished by the presence of a notochord, a dorsal hollow nerve cord, pharyngeal gill slits, and a muscular tail that extends past the anus. Vertebrates are distinguished by the presence of a cranium; most species also have vertebrae. In more derived groups of vertebrates, the body plan features an extensive endoskeleton composed of bone.

You should be able to sketch a sea star and a cephalochordate and label aspects of the body plan that qualify as synapomorphies.

MB **Web Animation** at www.masteringbio.com
Deuterostome Diversity

The diversification of echinoderms was triggered by the evolution of appendages called podia; the diversification of vertebrates was driven by the evolution of the jaw and limbs.

Most echinoderms move via their podia, and many species suspension feed, deposit feed, or act as predators with the aid of their podia.

Ray-finned fishes and tetrapods use their jaws to bite food and process it with teeth. Species in both groups move when muscles attached to their endoskeletons contract or relax. Tetrapods can move on land because their limbs enable walking, running, or flying. The evolution of the amniotic egg allowed tetrapods to lay eggs on land. Parental care was an important adaptation in some groups of ray-finned fishes and tetrapods—particularly mammals.

You should be able to explain why adaptations for efficient movement and feeding led to evolutionary success in terms of numbers and diversity of species in echinoderms and vertebrates.

Humans are a tiny twig on the tree of life. Chimpanzees and humans diverged from a common ancestor that lived in Africa 6–7 million years ago. Since then, at least 14 humanlike species have existed.

The fossil record of the past 3.5 million years contains at least 14 distinct species of hominins. Several of these organisms lived in Africa at the same time, and some lineages went extinct without leaving descendant populations. Thus, *Homo sapiens* is the sole surviving representative of an adaptive radiation. The phylogeny of living humans, based on comparisons of DNA sequences, agrees with evidence in the fossil record that *H. sapiens* originated in Africa and later spread throughout Europe, Asia, and the Americas. DNA sequences recovered from the fossilized bones of *H. neanderthalensis* suggest that *H. sapiens* replaced this species in Europe without interbreeding.

You should be able to describe evidence supporting the hypotheses that several species of hominin have lived at the same time and that *Homo sapiens* originated in Africa.

QUESTIONS

Test Your Knowledge

1. If you found an organism on a beach, what characteristics would allow you to declare that the organism is an echinoderm?
   a. radially symmetric adults, spines, and presence of tube feet
   b. notochord, dorsal hollow nerve cord, pharyngeal gill slits, and muscular tail
   c. exoskeleton and three pairs of appendages; distinct head and body (trunk) regions
   d. mouth that forms second (after the anus) during gastrulation

2. What is the diagnostic trait of vertebrates?
   a. skull
   b. jaws
   c. endoskeleton constructed of bone
   d. endoskeleton constructed of cartilage

3. Why are the pharyngeal jaws found in many ray-finned fishes important?
   a. They allow the main jaw to be protrusible (extendible).
   b. They make it possible for individuals to suck food toward their mouths.
   c. They give rise to teeth that are found on the main jawbones.
   d. They help process food.

4. Which of the following lineages make up the living Amniota?
   a. reptiles and mammals
   b. viviparous fishes
   c. frogs, salamanders, and caecilians
   d. hagfish, lampreys, and cartilaginous fishes (sharks and rays)

5. Which of the following does *not* occur in either cartilaginous fishes or ray-finned fishes?
   a. internal fertilization and viviparity or ovoviviparity
   b. external fertilization and oviparity
   c. formation of a placenta
   d. feeding of young

6. Most species of hominins are known only from Africa. Which species have been found in other parts of the world as well?
   a. early *Homo*—*H. habilis* and *H. ergaster*
   b. *H. erectus*, *H. neanderthalensis*, and *H. floresiensis*
   c. gracile australopithecines
   d. robust australopithecines

Test Your Knowledge answers: 1. a; 2. a; 3. d; 4. a; 5. d; 6. b

Test Your Understanding

Answers are available at www.masteringbio.com

1. Explain how the water vascular system of echinoderms functions as a type of hydrostatic skeleton.

2. List the four morphological traits that distinguish chordates. How are these traits involved in locomotion and feeding in larvae or adults?

3. Describe evidence that supports the hypothesis that jaws evolved from gill arches in fish.

4. Describe evidence that supports the hypothesis that the tetrapod limb evolved from the fins of lobe-finned fishes.

5. The text claims that "*Homo sapiens* is the sole survivor of an adaptive radiation that took place over the past 7 million years." Do you agree with this statement? Why or why not? Identify three major trends in the evolution of hominins, and suggest a hypothesis to explain each.

6. Explain how the evolution of the placenta and lactation in mammals improved the probability that their offspring would survive. Over the course of a lifetime, why are female mammals expected to produce fewer eggs than do female fish?

Applying Concepts to New Situations

Answers are available at www.masteringbio.com

1. Describe the conditions under which it might be possible for a new species of *Homo* to evolve from current populations of *H. sapiens*.
2. Compare and contrast adaptations that triggered the diversification of the three most species-rich animal lineages: molluscs, arthropods, and vertebrates.
3. Aquatic habitats occupy 73 percent of Earth's surface area. How does this fact relate to the success of ray-finned fishes? How does it relate to the success of coelacanths and other lobe-finned fishes?
4. Mammals and birds are endothermic. Did they inherit this trait from a common ancestor, or did endothermy evolve independently in these two lineages? Provide evidence to support your answer.