Unit 4 MECHANISMS OF EVOLUTION



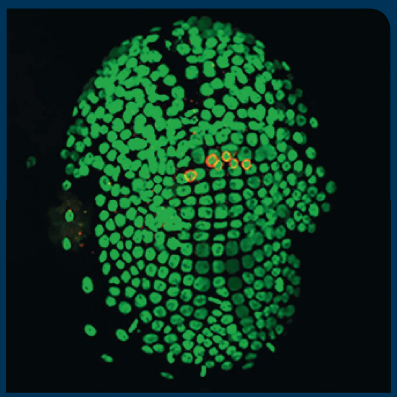
Cassandra Extavour is Professor in the Department of Organismic and Evolutionary Biology at Harvard University, where she and her students are studying genes that control early embryonic development, as well as the evolutionary origins of these genes and how their functions have changed over time. Born in Toronto, Canada, Dr. Extavour received a B.Sc. (honors) in Molecular Biology and Genetics from the University of Toronto, followed by a Ph.D. in the same subject area from Universidad Autónoma de Madrid, Spain. After completing two postdoctoral fellowships (one in Greece, the other in the United Kingdom), she worked for several years as a Research Associate at Cambridge University, UK, before joining the faculty at Harvard. Dr. Extavour is a dedicated advocate for women and underrepresented groups in science, and she also has performed worldwide as a professional soprano.

AN INTERVIEW WITH

Cassandra Extavour

How did you first become interested in science?

Although my first love was music, and music remains an essential part of my life, toward the end of high school I also became quite interested in biology. My conversations with a friend who was fascinated by human behavior led me to wonder how the brain causes people to exhibit different behaviors. But how could I learn about that? My parents did not go to college. I didn't even know that there were careers in science that were not in medicine. I thought the only way to learn about the brain was to be a doctor. So I entered university as a pre-med. But by the time I was finishing my undergraduate studies, I had learned about research labs. I got a summer internship in a developmental genetics lab, and I loved it—it was like entering a new world where I could figure out the answers to questions that interested me.



▲ Embryo of the crustacean *Parhyale hawaiensis* showing cells (in red) that will develop into germ cells

What are the main questions you are asking in your research?

I'm interested in understanding the genes that control embryonic development and how the function of those genes has changed in different organisms due to evolution. Take a human, for example. Our bodies have many different types of cells. The instructions for everything that each of our cells needs to do are contained in the cell's DNA. All of our cells have exactly same DNA. What's mysterious is, since every cell in the body has the same set of instructions, why aren't they all doing the same thing? I work mostly with insects, but the same question applies to them (and to all multicellular organisms). We're trying to figure out how the same set of genes is used in different ways by different cells. We're also interested in where these genes came from in the first place and how they have evolved over time.

Much of your research has been on "evo-devo." Say more about what that means.

Evo-devo stands for evolutionary developmental biology. Scientists in this field try to understand the difference in development between, let's say, a coconut and a rose. They're both plants, they both make seeds, they both make pollen, but they don't look the same at all. Why is that? Or the fact that, when you compare the development of a monkey and a human, you can't detect many differences in their embryos or their genes. How can they be similar in so many ways and yet end up as such different organisms? In my lab, we are particularly interested in egg and sperm cells—known as germ cells. We're trying to figure out how an embryo determines which cells become germ cells and how it tells those cells, "Okay, listen: When the animal you are part of becomes an adult, you will need to make eggs and sperm." We've found that in some cases, the same genes are used by a variety of different species to make germ cells. But in other cases, we've been surprised to find that a gene used to produce germ cells in one organism is used to make a completely different type of cell in another closely related organism.

"What's mysterious is, since every cell in the body has the same set of instructions, why aren't they all doing the same thing?"

What do you find most rewarding about your job?

When I was in high school, I never would have thought that I could get paid to think of interesting questions and then try to answer them. I love doing that, and I love the amazing freedom that comes with my job—I get to decide what I'm going to do each day. But the best part is working with students as they gain the independence, knowledge, and confidence to listen to my suggestions and then say, "I'm not sure that's the best experiment. Here's an experiment that I think would be better, and here's why." That is a great moment. What they are really saying is, "I'm not learning to be a scientist anymore—I am a scientist." They've come to understand what scientists do: We make the best proposal we can, we test it as best we can, and we say, "This is what I think the results from my experiments mean."

22 Descent with Modification: A Darwinian View of Life

KEY CONCEPTS

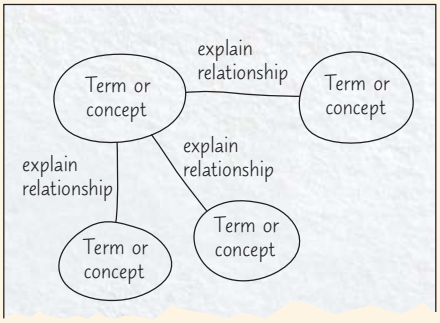
22.1 **The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species** *p. 469*

22.2 **Descent with modification by natural selection explains the adaptations of organisms and the unity and diversity of life** *p. 471*

22.3 **Evolution is supported by an overwhelming amount of scientific evidence** *p. 476*

Study Tip

Make a word cloud: This chapter covers key topics related to evolution, such as descent with modification, heritable characteristics, natural selection, adaptation, convergent evolution, homology, and unity of life. Draw a "word cloud" of these terms: As you read the chapter, draw a line between terms that affect or relate to one another. Next to that line, briefly explain how those terms are connected.



Go to Mastering Biology

For Students (in eText and Study Area)
- Get Ready for Chapter 22
- Figure 22.17 Walkthrough: Tree Thinking
- Figure 22.20 Walkthrough: Transition to Life in the Sea
- BBC Video: A Future Without Antibiotics?

For Instructors to Assign (in Item Library)
- HHMI Video: The Making of the Fittest: Natural Selection and Adaptation (Pocket Mouse)



Figure 22.1 This Malaysian orchid mantis (*Hymenopus coronatus*) closely resembles the flower on which it rests, waiting for unwary prey to come within its reach. Other mantises have diverse shapes and colors that have evolved in different environments—yet all mantises also share certain features, such as grasping forelimbs, large eyes, and six legs.

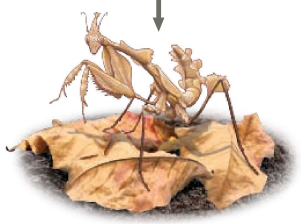
What causes the similarities and differences among Earth's many different species?



Ancient common ancestor

Species accumulate differences from their ancestors as they **adapt to different environments** over many generations.







While different in some ways, these species share many similar features because they descended from a common ancestor. This process of

descent with modification

shared ancestry, resulting in shared characteristics

accumulation of differences

has given rise to the **diversity of life**.

CONCEPT 22.1

The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species

More than a century and a half ago, Charles Darwin was inspired to develop a scientific explanation for the *diversity of life*, the great number and remarkable variety of species on Earth. When he published his hypothesis in his book *The Origin of Species*, Darwin ushered in a scientific revolution—the era of evolutionary biology. As we'll see, Darwin developed his revolutionary ideas over time, influenced by the work of others and his travels **(Figure 22.2)**.

Endless Forms Most Beautiful

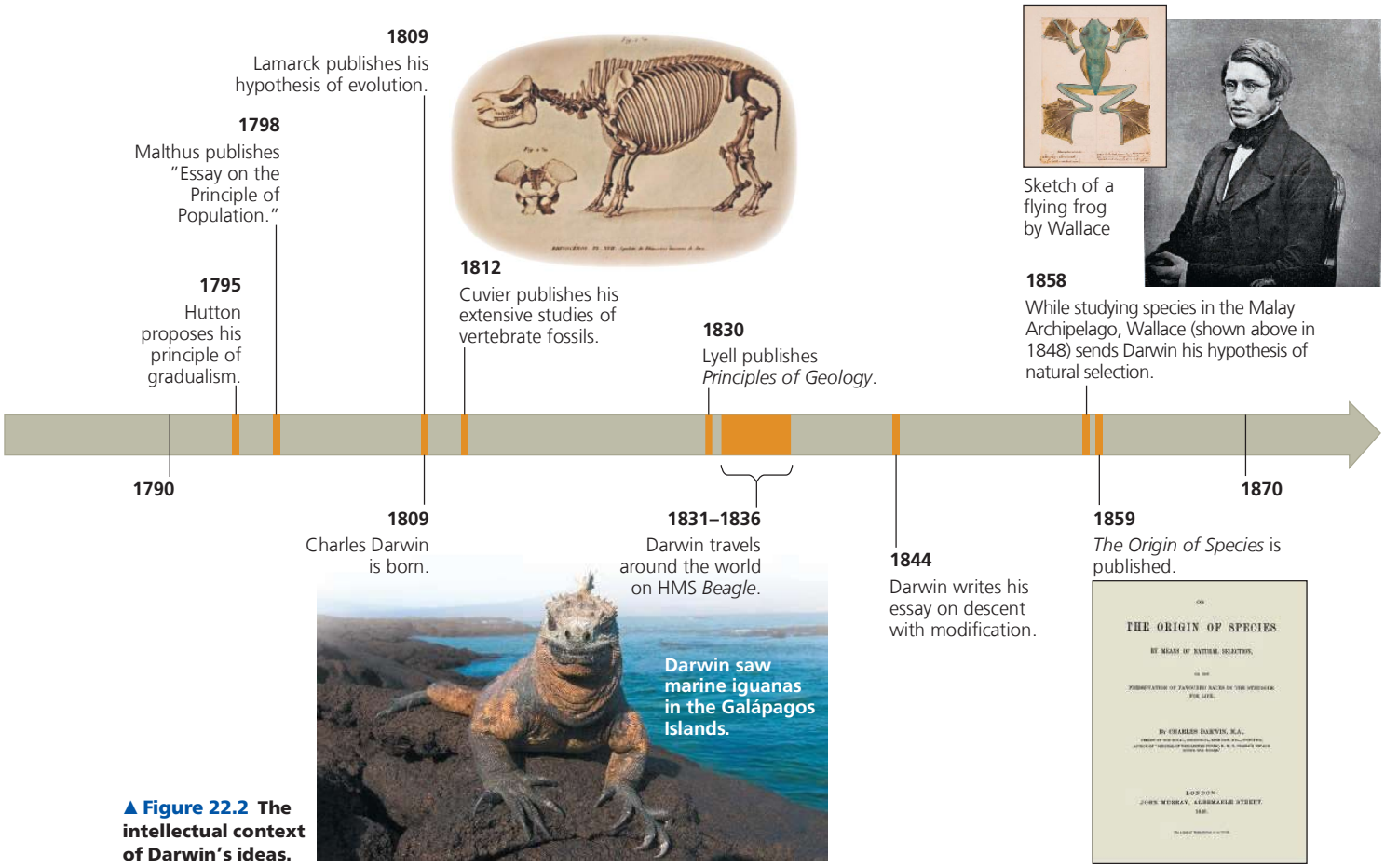
To set the stage for our study of Darwin and evolutionary biology, let's return to the well-hidden orchid mantis in Figure 22.1. This species is a member of a diverse group of insects, the Mantodea, which includes 2,300 species in 430 genera. All these mantises share certain features, such as three pairs of legs, triangular heads with bulging eyes, and a flexible "neck." Such shared features illustrate the unity of life, a phrase that highlights the fact that all organisms share characteristics.

But Earth's many different species also differ from one another. The mantises, for example, differ in features such as their size, shape, and color. Overall, the orchid mantis and its many close relatives illustrate three key observations about life:

- organisms are well suited (adapted) for life in their environments (Here and throughout this text, the term *environment* refers to other organisms as well as to the physical aspects of an organism's surroundings.)
- the many shared characteristics (unity) of life
- the rich diversity of life

Darwin, a keen observer of nature since childhood, set out to explain these three broad observations—an effort that eventually led him to conclude that life evolves over time.

For now, we will define **evolution** as *descent with modification*, a phrase Darwin used to summarize the process



▲ Figure 22.2 The intellectual context of Darwin's ideas.

by which species accumulate differences from their ancestors as they adapt to different environments over time. Evolution can also be defined as a change in the genetic composition of a population from generation to generation (see Concept 23.3).

However it is defined, we can view evolution in two related but different ways: as a pattern and as a process. The *pattern* of evolutionary change is revealed by data from many scientific disciplines, including biology, geology, physics, and chemistry. These data are facts—they are observations about the natural world—and these observations show that life has evolved over time. The *process* of evolution consists of the mechanisms that cause the observed pattern of change. These mechanisms represent natural causes of the natural phenomena we observe. Indeed, the power of evolution as a unifying theory is its ability to explain and connect a vast array of observations about the living world.

As with all general theories in science, we continue to test our understanding of evolution by examining whether it can account for new observations and experimental results. In this and the following chapters, we'll examine how ongoing discoveries shape what we know about the pattern and process of evolution.

We'll begin our exploration of these discoveries by retracing Darwin's quest to explain the adaptations, unity, and diversity of what he called life's "endless forms most beautiful."

Scala Naturae and Classification of Species

Long before Darwin was born, several Greek philosophers suggested that life might have changed gradually over time. But one philosopher who greatly influenced early Western science, Aristotle (384–322 BCE), viewed species as fixed (unchanging). Through his observations of nature, Aristotle recognized certain "affinities" among organisms. He concluded that life-forms could be arranged on a ladder, or scale, of increasing complexity, later called the *scala naturae* ("scale of nature"). Each form of life, perfect and permanent, had its allotted rung on this ladder.

These ideas were generally consistent with the Old Testament account of creation, which holds that species were individually designed by God and therefore perfect. In the 1700s, many scientists interpreted the often remarkable ways in which organisms are well suited for life in their environment as evidence that the Creator had designed each species for a particular purpose.

One such scientist was Carolus Linnaeus (1707–1778), a Swedish physician and botanist who sought to classify life's diversity, in his words, "for the greater glory of God." In the 1750s, Linnaeus developed the two-part, or *binomial*, format for naming species (such as *Homo sapiens* for humans) that is still used today. In contrast to the linear hierarchy of the *scala naturae*, Linnaeus used a nested classification system, grouping similar species into increasingly inclusive categories. For example, similar species are grouped in the same genus, similar genera (plural of genus) are grouped in the same family, and so on.

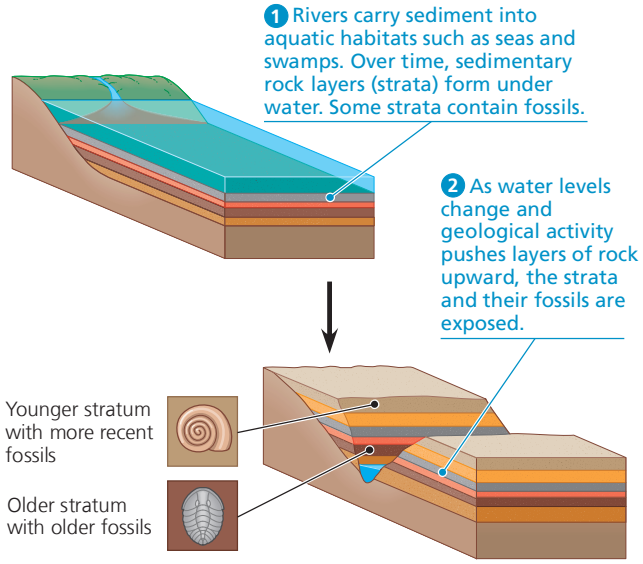
Linnaeus did not ascribe the resemblances among species to evolutionary kinship, but rather to the pattern of their creation. A century later, however, Darwin argued that classification should be based on evolutionary relationships. He also noted that scientists using the Linnaean system often grouped organisms in ways that reflected those relationships.

Ideas About Change over Time

Among other sources of information, Darwin drew from the work of scientists studying **fossils**, the remains or traces of organisms from the past. Many fossils are found in sedimentary rocks formed from the sand and mud that settle to the bottom of seas, lakes, and swamps **(Figure 22.3)**. New layers of sediment cover older ones and compress them into superimposed layers of rock called **strata** (singular, *stratum*). The fossils in a particular stratum provide a glimpse of some of the organisms that populated Earth at the time that layer formed. Later, erosion may carve through upper (younger) strata, revealing deeper (older) strata that had been buried.

Paleontology, the study of fossils, was developed in large part by French scientist Georges Cuvier (1769–1832). In examining strata near Paris, Cuvier noted that the older the stratum, the more dissimilar its fossils were to current life-forms. He also observed that from one layer to the next, some new species appeared while others disappeared. He inferred that extinctions must have been a common occurrence, but he staunchly opposed the idea of evolution. Cuvier speculated that each boundary between strata represented a sudden catastrophic

▼ Figure 22.3 Formation of sedimentary strata with fossils.



Mastering Biology Video: Grand Canyon

event, such as a flood, that had destroyed many of the species living in that area. Such regions, he reasoned, were later repopulated by different species immigrating from other areas.

In contrast to Cuvier's emphasis on sudden events, other scientists suggested that profound change could take place through the cumulative effect of slow but continuous processes. In 1795, Scottish geologist James Hutton (1726–1797) proposed that Earth's geologic features could be explained by gradual mechanisms, such as valleys being formed by rivers. The leading geologist of Darwin's time, Charles Lyell (1797–1875), incorporated Hutton's thinking into his proposal that the same geologic processes are operating today as in the past, and at the same rate.

Hutton's and Lyell's ideas strongly influenced Darwin's thinking. Darwin agreed that if geologic change results from slow, continuous actions rather than from sudden events, then Earth must be much older than the widely accepted age of a few thousand years. It would, for example, take a very long time for a river to carve a canyon by erosion. He later reasoned that perhaps similarly slow and subtle processes could produce substantial biological change. However, Darwin was not the first to apply the idea of gradual change to biological evolution.

Lamarck's Hypothesis of Evolution

Although some 18th-century naturalists suggested that life evolves as environments change, only one proposed a mechanism for *how* life changes over time: French biologist Jean-Baptiste de Lamarck (1744–1829). Alas, Lamarck is primarily remembered today *not* for his visionary recognition that evolutionary change explains patterns in fossils and how organisms are well suited for their environments, but for the incorrect mechanism he proposed.

Lamarck published his hypothesis in 1809, the year Darwin was born. By comparing living species with fossil forms, Lamarck had found what appeared to be several lines of descent, each a chronological series of older to younger fossils leading to a living species. He explained his findings using two principles that were widely accepted at the time. The first was *use and disuse*, the idea that parts of the body that are used extensively become larger and stronger, while those that are not used deteriorate. Among many examples, he cited a giraffe stretching its neck to reach leaves on high branches. The second principle, *inheritance of acquired characteristics*, stated that an organism could pass these modifications to its offspring. Lamarck reasoned that the long, muscular neck of the living giraffe had evolved over many generations as giraffes stretched their necks ever higher.

Lamarck also thought that evolution happens because organisms have an innate drive to become more complex. Darwin rejected this idea, but he, too, thought that variation was introduced into the evolutionary process in part by inheritance of acquired characteristics. Today, however, our understanding of genetics refutes this mechanism: Experiments show that traits acquired by use during an individual's life are not inherited in the way proposed by Lamarck **(Figure 22.4)**.



▶ Figure 22.4 Acquired traits cannot be inherited. This bonsai tree was "trained" to grow as a dwarf by pruning and shaping. However, seeds from this tree would produce offspring of normal size.

Lamarck was vilified in his own time, especially by Cuvier, who denied that species ever evolve. In retrospect, however, Lamarck did recognize that the fact that organisms are well-suited for life in their environments can be explained by gradual evolutionary change, and he did propose a testable explanation for how this change occurs.

CONCEPT CHECK 22.1

1. How did Hutton's and Lyell's ideas influence Darwin's thinking about evolution?
2. **MAKE CONNECTIONS** Scientific hypotheses must be testable (see Concept 1.3). Applying this criterion, are Cuvier's explanation of the fossil record and Lamarck's hypothesis of evolution scientific? Explain your answer in each case.

For suggested answers, see Appendix A.

CONCEPT 22.2

Descent with modification by natural selection explains the adaptations of organisms and the unity and diversity of life

As the 19th century dawned, it was generally thought that species had remained unchanged since their creation. A few clouds of doubt about the permanence of species were beginning to gather, but no one could have forecast the thundering storm just beyond the horizon. How did Charles Darwin become the lightning rod for a revolutionary view of life?

Darwin's Research

Charles Darwin (1809–1882) was born in Shrewsbury, in western England. Even as a boy, he had a consuming interest in nature. When he was not reading nature books, he was fishing, hunting, riding, and collecting insects. However,

Darwin's father, a physician, could see no future for his son as a naturalist and sent him to medical school in Edinburgh. But Charles found medicine boring and surgery before the days of anesthesia horrifying. He quit medical school and enrolled at Cambridge University, intending to become a clergyman. (At that time, many scholars of science belonged to the clergy.)

At Cambridge, Darwin became the protégé of John Henslow, a botany professor. Soon after Darwin graduated, Henslow recommended him to Captain Robert FitzRoy, who was readying the survey ship HMS *Beagle* for a voyage around the world. Darwin would pay his own way and serve as a conversation partner to the young captain. FitzRoy, who was himself an adept scientist, accepted Darwin because he was a skilled naturalist and they were of similar age and social class.

The Voyage of the Beagle

Darwin embarked from England on the *Beagle* in December 1831. The primary mission of the voyage was to chart stretches of the South American coast that were poorly known to Europeans. Darwin, however, spent most of his time on shore, observing and collecting thousands of plants and animals. He described features of organisms that made them well suited to such diverse environments as the humid jungles of Brazil, the expansive grasslands of Argentina, and the towering peaks of the Andes. He also noted that the plants and animals in temperate regions of South America more closely resembled species living in the South American tropics than species living in temperate regions of Europe. Furthermore, the fossils he found, though clearly different from living species, distinctly resembled the living organisms of South America.

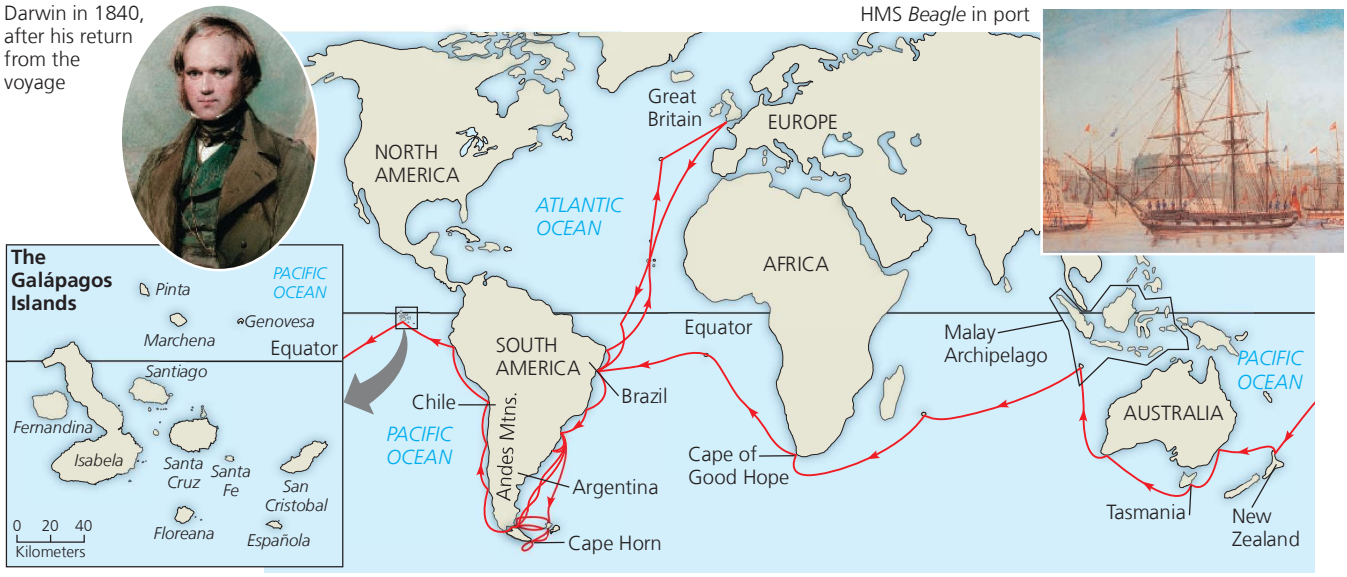
Darwin also spent much time thinking about geology. Despite repeated bouts of seasickness, he read Lyell's *Principles of Geology* during the voyage. He experienced geologic change firsthand when a violent earthquake shook the coast of Chile, and he observed afterward that rocks along the coast had been thrust upward by several meters. Finding fossils of ocean organisms high in the Andes, Darwin inferred that the rocks containing the fossils must have been raised there by many similar earthquakes. These observations reinforced what he had learned from Lyell: Physical evidence did not support the traditional view that Earth was only a few thousand years old.

Darwin's interest in the species (or fossils) found in an area was further stimulated by the *Beagle*'s stop at the Galápagos, a group of volcanic islands located near the equator about 900 km west of South America **(Figure 22.5)**. Darwin was fascinated by the unusual organisms there. The birds he collected included several kinds of mockingbirds. These mockingbirds, though similar to each other, seemed to be different species. Some were unique to individual islands, while others lived on two or more adjacent islands. Furthermore, although the animals on the Galápagos resembled species living on the South American mainland, most of the Galápagos species were not known from anywhere else in the world. Darwin hypothesized that the Galápagos had been colonized by organisms that had strayed from South America and then diversified, giving rise to new species on the various islands.

Darwin's Focus on Adaptation

During the voyage of the *Beagle*, Darwin observed many examples of **adaptations**, inherited characteristics of organisms that enhance their survival and reproduction in specific environments. Later, as he reassessed his observations, he began to perceive adaptation to the environment and the origin of new species as closely related processes. Could a new species arise

▼ Figure 22.5 The voyage of HMS *Beagle* (December 1831–October 1836).



▼ Figure 22.6 Three examples of beak variation in Galápagos finches. The Galápagos Islands are home to more than a dozen species of closely related finches, some found only on a single island. A striking difference among them is their beaks, which are adapted for specific diets.



(a) Cactus-eater. The long, sharp beak of the common cactus finch (*Geospiza scandens*) helps it tear and eat cactus flowers and pulp.



(b) Insect-eater. The green warbler finch (*Certhidea olivacea*) uses its narrow, pointed beak to grasp insects.



(c) Seed-eater. The large ground finch (*Geospiza magnirostris*) has a large beak adapted for cracking seeds found on the ground.

MAKE CONNECTIONS *Review Figure 1.20. Circle the most recent common ancestor shared by the three species that eat insects. Are all of the descendants of that ancestor insect-eaters?*

from an ancestral form by the gradual accumulation of adaptations to a different environment? From studies made years after Darwin's voyage, biologists have concluded that this is indeed what happened to a diverse group of finches found on the Galápagos Islands (see Figure 1.20). The finches' various beaks and behaviors are adapted to the specific foods available on their home islands **(Figure 22.6)**. Darwin realized that explaining such adaptations was essential to understanding evolution. His explanation of how adaptations arise centered on **natural selection**, a process in which individuals that have certain inherited traits tend to survive and reproduce at higher rates than do other individuals *because of* those traits. By the early 1840s, Darwin had worked out the major features of his hypothesis. He set these ideas on paper in 1844, when he wrote a long essay on descent with modification and its underlying mechanism, natural selection. Yet he was still reluctant to publish his ideas, in part because he anticipated the uproar they would cause. During this time, Darwin continued to compile evidence in support of his hypothesis. By the mid-1850s, he had described his ideas to Lyell and a few others. Lyell, who was not yet convinced of evolution, nevertheless urged Darwin to publish on the subject before someone else came to the same conclusions and published first.

In June 1858, Lyell's prediction came true. Darwin received a manuscript from Alfred Russel Wallace (1823–1913), a British naturalist working in the South Pacific islands of the Malay Archipelago (see Figure 22.2). Wallace had developed a hypothesis of natural selection nearly identical to Darwin's. He asked Darwin to evaluate his paper and forward it to Lyell if it merited publication. Darwin complied, writing to Lyell: "Your words have come true with a vengeance.... I never saw a more striking coincidence... so all my originality, whatever it may amount to, will be smashed." On July 1, 1858, Lyell and a colleague presented Wallace's paper, along with extracts from Darwin's unpublished 1844 essay, to the Linnean Society of London. Darwin quickly finished his book, titled *On the Origin of Species by Means of Natural Selection* (commonly referred to as *The Origin of Species*), and published it the next year. Although Wallace had submitted his ideas for publication first, he admired Darwin and thought that Darwin had developed and tested the idea of natural selection so extensively that he should be known as its main architect.

Within a decade, Darwin's book and its proponents had convinced most scientists that life's diversity is the product of evolution. Darwin succeeded where previous evolutionists had failed by presenting a plausible scientific mechanism with immaculate logic and an avalanche of supporting evidence.

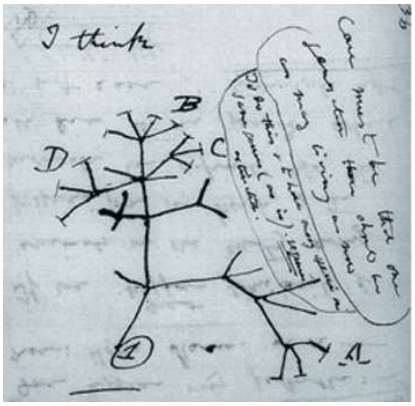
Mastering Biology **HHMI Video: The Origin of Species: The Making of a Theory**

Ideas from *The Origin of Species*

In his book, Darwin amassed evidence that descent with modification by natural selection explains three broad observations about nature—the unity of life, the diversity of life, and the striking ways in which organisms are suited for life in their environments.

Descent with Modification

In the first edition of *The Origin of Species*, Darwin never used the word *evolution* (although the final word of the book is "evolved"). Rather, he discussed *descent with modification*, a phrase that summarized his view of life. Organisms share many characteristics, leading Darwin to perceive unity in life. He attributed the unity of life to the descent of all organisms from an ancestor that lived in the remote past. He also thought that as the descendants of that ancestral organism lived in various habitats, they gradually accumulated diverse modifications, or adaptations, that fit them to specific ways of life. Thus, Darwin thought of evolution as a process in which both *descent* (shared ancestry, resulting in shared characteristics) and *modification* (the accumulation of differences) can be observed.



▶ Figure 22.7 "I think . . . ." In this 1837 sketch, Darwin envisioned the branching pattern of evolution. Branches that end in twigs labeled A–D represent particular groups of living organisms; all other branches represent extinct groups.

Darwin reasoned that over a long period of time, descent with modification eventually led to the rich diversity of life we see today. He viewed the history of life as a tree, with multiple branchings from a common trunk out to the tips of the youngest twigs **(Figure 22.7)**. In his diagram, the tips of the twigs that are labeled A–D represent several groups of organisms living in the present day, while the unlabeled branches represent groups that are extinct. Each fork of the tree represents the most recent common ancestor of all the lines of evolution that subsequently branch from that point.

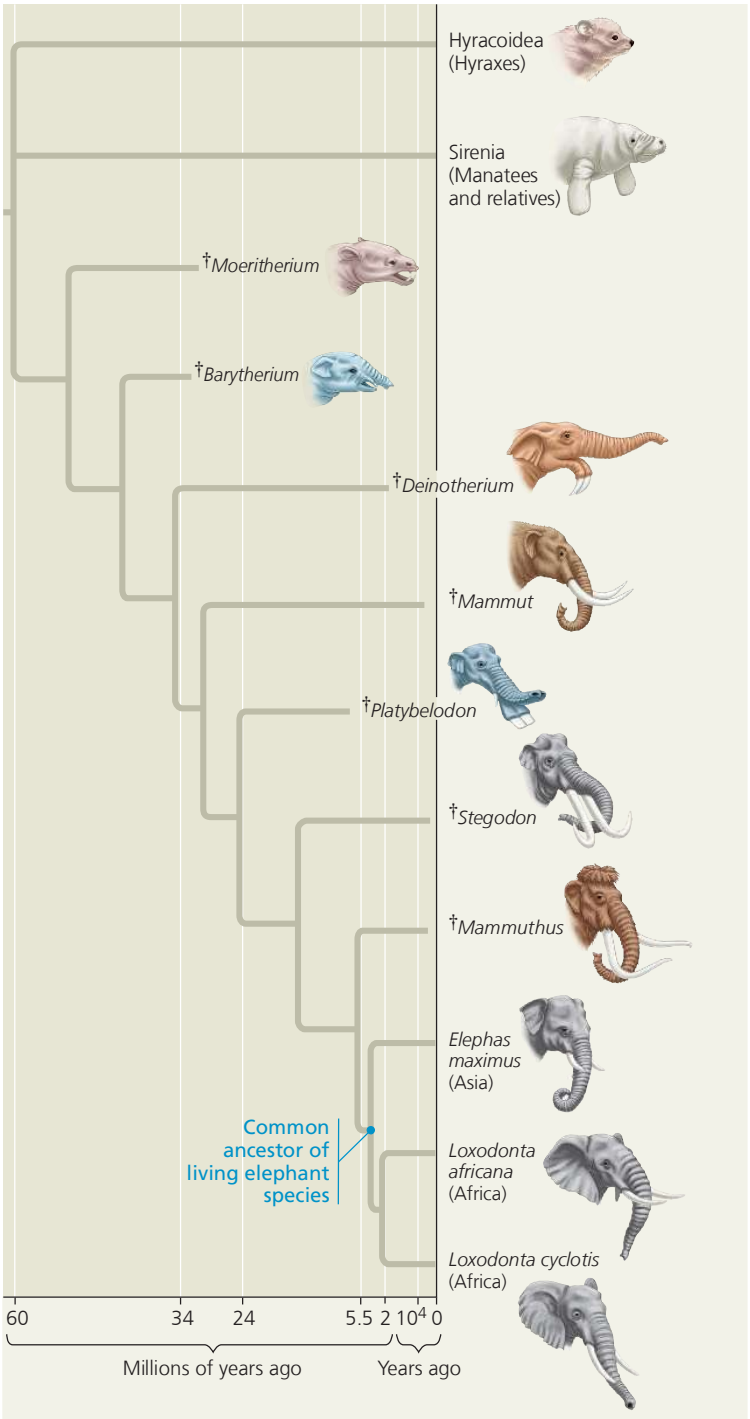
Darwin thought that such a branching process, along with past extinction events, could explain the large morphological gaps that sometimes exist between related groups of organisms. As an example, let's consider the three living species of elephants: the Asian elephant (*Elephas maximus*) and two species of African elephants (*Loxodonta africana* and *L. cyclotis*). These closely related species are very similar because they shared the same line of descent until a relatively recent split from their common ancestor, as shown in the tree diagram in **Figure 22.8**. Note that seven lineages related to elephants have become extinct over the past 32 million years. As a result, there are no living species that fill the morphological gap between the elephants and their nearest relatives today, the hyraxes and manatees.

Extinctions like those in Figure 22.8 are common. In fact, many evolutionary branches, even some major ones, are dead ends: Scientists estimate that over 99% of all species that have ever lived are now extinct. As in Figure 22.8, fossils of extinct species can document the divergence of present-day groups by "filling in" gaps between them.

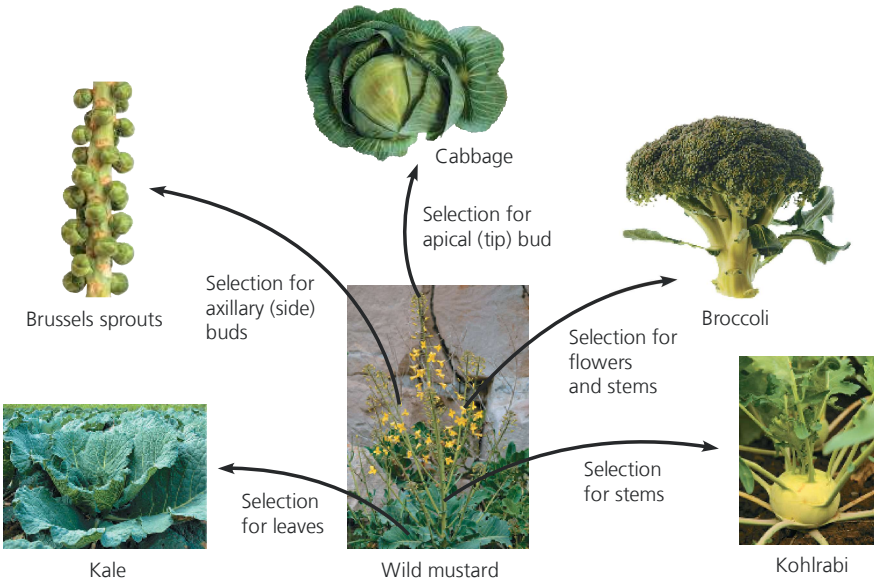
Artificial Selection, Natural Selection, and Adaptation

Darwin proposed the mechanism of natural selection to explain the observable patterns of evolution. He crafted his argument carefully, hoping to persuade even the most skeptical readers. First he discussed familiar examples of selective breeding of domesticated plants and animals. Humans have modified other species over many generations by selecting and breeding individuals that possess desired traits, a process

▼ Figure 22.8 Descent with modification. This evolutionary tree of elephants and their relatives is based mainly on fossils—their anatomy, order of appearance in strata, and geographic distribution. Note that most branches of descent ended in extinction (denoted by the dagger symbol, †). (Time line not to scale.)



VISUAL SKILLS *Based on this tree, approximately when did the most recent ancestor shared by* Mammuthus *(woolly mammoths), Asian elephants, and African elephants live?*



▶ **Figure 22.9 Artificial selection.** These different vegetables have all been selected from one species of wild mustard (*Brassica oleracea*). By selecting variations in different parts of the plant, breeders have obtained these divergent results.

called **artificial selection** **(Figure 22.9)**. As a result of artificial selection, crops, livestock animals, and pets often bear little resemblance to their wild ancestors.

Darwin then argued that a similar process occurs in nature. He based his argument on two observations, from which he drew two inferences:

Observation #1: Members of a population often vary in their inherited traits **(Figure 22.10)**.

Observation #2: All species can produce more offspring than their environment can support **(Figure 22.11)**, and many of these offspring fail to survive and reproduce.

Inference #1: Individuals whose inherited traits give them a higher probability of surviving and reproducing in a given environment tend to leave more offspring than do other individuals.

Inference #2: This unequal ability of individuals to survive and reproduce will lead to the accumulation of favorable traits in the population over generations.

As these two inferences suggest, Darwin saw a connection between natural selection and the capacity of organisms to "overreproduce." He began to make this connection after reading an essay by economist Thomas Malthus, who contended that much of human suffering—disease, famine, and war—resulted from the human population's potential to increase faster than food supplies and other resources. Darwin similarly realized that the capacity to overreproduce was typical of all species. Of the many eggs laid, young born, and seeds spread, only a fraction complete their development and leave offspring of their own. The rest are starved, eaten, diseased, unmated, or unable to tolerate physical conditions of the environment such as salinity or temperature.

An organism's heritable traits can influence not only its own performance, but also how well its offspring cope with

▼ **Figure 22.10 Variation in a population.** Individuals in this population of Asian ladybird beetles (*Harmonia axyridis*) vary in color and spot pattern. Natural selection may act on these variations only if (1) they are heritable and (2) they affect the beetles' ability to survive and reproduce.



▶ **Figure 22.11 Overproduction of offspring.** A single puffball fungus can produce billions of spores that give rise to offspring. If all of these offspring and their descendants survived to maturity, they would carpet the surrounding land surface.



environmental challenges. For example, an organism might have a trait that gives its offspring an advantage in escaping predators, obtaining food, or tolerating physical conditions. When such advantages increase the number of offspring that survive and reproduce, the traits that are favored will likely appear at a greater frequency in the next generation. Thus, over time, natural selection resulting from factors such as predators, lack of food, or adverse physical conditions can lead to an increase in the proportion of favorable traits in a population.

How rapidly do such changes occur? Darwin reasoned that if artificial selection can bring about dramatic change in a relatively short period of time, then natural selection should be capable of substantial modification of species over many hundreds of generations. Even if the advantages of some heritable traits over others are slight, the advantageous variations will gradually accumulate in the population, and less favorable variations will diminish. Over time, this process will increase the frequency of individuals with favorable adaptations, hence increasing the degree to which organisms are well suited for life in their environment.

Key Features of Natural Selection

Let's now summarize some of the main ideas of natural selection:

- Natural selection is a process in which individuals that have certain heritable traits survive and reproduce at a higher rate than do other individuals because of those traits.
- Over time, natural selection can increase the frequency of adaptations that are favorable in a given environment **(Figure 22.12)**.
- If an environment changes, or if individuals move to a new environment, natural selection may result in adaptation to these new conditions, sometimes giving rise to new species.

One subtle but important point is that although natural selection occurs through interactions between individual organisms and their environment, *individuals do not evolve*. Rather, it is the population that evolves over time.

A second key point is that natural selection can amplify or diminish only those heritable traits that differ among the individuals in a population. Thus, even if a trait is heritable, if all the individuals in a population are genetically identical for that trait, evolution by natural selection cannot occur.

Third, environmental factors vary from place to place and over time. A trait that is favorable in one place or time may be useless—or even detrimental—in other places or times. Natural selection is always operating, but which traits are favored depends on the context in which a species lives and mates.

Next, we'll survey the wide range of observations that support a Darwinian view of evolution by natural selection.



▲ Figure 22.12 Camouflage as an example of evolutionary adaptation. Related species of moths have diverse shapes and colors that evolved in different environments, as seen in this dead-leaf moth (*Oxytenis modestia*) in Peru **(a)** and buff-end moth (*Phalera bucephala*) in Scotland **(b)**.

CONCEPT CHECK 22.2

1. How does the concept of descent with modification explain both the unity and diversity of life?
2. **WHAT IF?** If you discovered a fossil of an extinct mammal that lived high in the Andes, would you predict that it would more closely resemble present-day mammals from South American jungles or present-day mammals that live high in Asian mountains? Explain.
3. **MAKE CONNECTIONS** Review the relationship between genotype and phenotype (see Figures 14.5 and 14.6). Suppose that in a particular pea population, flowers with the white phenotype are favored by natural selection. Predict what would happen over time to the frequency of the white-flower allele (the *p* allele) in the population.

For suggested answers, see Appendix A.

CONCEPT 22.3

Evolution is supported by an overwhelming amount of scientific evidence

In *The Origin of Species*, Darwin marshaled a broad range of evidence to support the concept of descent with modification. Still—as he readily acknowledged—there were instances

in which key evidence was lacking. For example, Darwin referred to the origin of flowering plants as an "abominable mystery," and he lamented the lack of fossils showing how earlier groups of organisms gave rise to new groups.

In the last 150 years, new discoveries have filled many of the gaps that Darwin identified. The origin of flowering plants, for example, is much better understood (see Concept 30.3), and many fossils have been discovered that signify the origin of new groups of organisms (see Concept 25.2). In this section, we'll consider four types of data that document the pattern of evolution and illuminate how it occurs: direct observations, homology, the fossil record, and biogeography.

Direct Observations of Evolutionary Change

Biologists have documented evolutionary change in thousands of scientific studies. We'll examine many such studies throughout this unit, but let's look at two examples here.

Natural Selection in Response to Introduced Species

Herbivores, animals that eat plants, often have adaptations that help them feed efficiently on their primary food sources. What happens when herbivores switch to a new food source with different characteristics?

An opportunity to study this question in nature is provided by soapberry bugs, which use their "beak"—a hollow, needlelike mouthpart—to feed on seeds located within the fruits of various plants. In southern Florida, the soapberry bug (*Jadera haematoloma*) feeds on the seeds of a native plant, the balloon vine (*Cardiospermum corindum*). In central Florida, however, where balloon vines have become rare, soapberry bugs feed on the seeds of the golden rain tree (*Koelreuteria elegans*), a species recently introduced from Asia.

Soapberry bugs feed most effectively when the length of their beak is similar to the depth at which seeds are found within the fruit. Golden rain tree fruit consists of three flat lobes, and its seeds are much closer to the fruit surface than are the seeds of the plump, round fruit of the native balloon vine. These differences led researchers to predict that in populations that feed on golden rain tree, natural selection would result in beaks that are *shorter* than those in populations that feed on balloon vine **(Figure 22.13)**. Indeed, beak lengths are shorter in the populations that feed on golden rain tree.

Researchers have also studied beak length evolution in soapberry bug populations that feed on plants introduced to Louisiana, Oklahoma, and Australia. In each of these locations, the fruit of the introduced plants is larger than the fruit of the native plant. Thus, in populations feeding on introduced species in these regions, researchers predicted that natural selection would result in the evolution of *longer* beaks. Again, data collected in field studies upheld this prediction.

The observed changes in beak lengths had important consequences. In Australia, for example, the increase in beak

▼ Figure 22.13 Inquiry

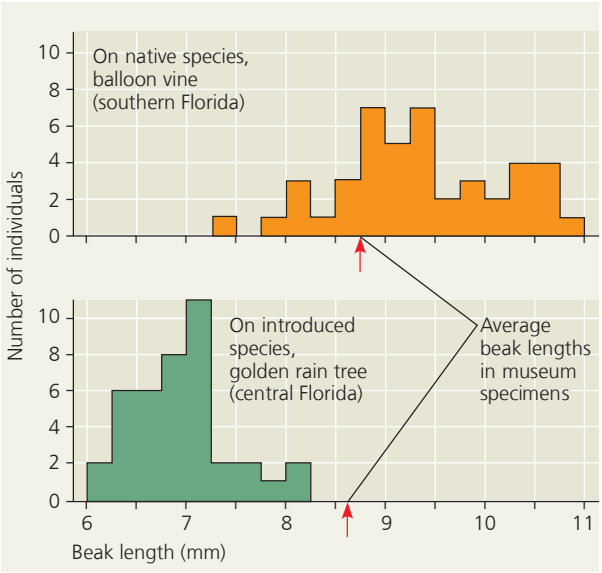
Can a change in a population's food source result in evolution by natural selection?

Field Study Soapberry bugs feed most effectively when the length of their "beak" is similar to the depth of the seeds within the fruit. Researchers measured beak lengths in soapberry bug populations feeding on the native balloon vine. They also measured beak lengths in populations feeding on the introduced golden rain tree. The researchers then compared the measurements with those of museum specimens collected in the two areas before the golden rain tree was introduced.



Soapberry bug with beak inserted in balloon vine fruit

Results Beak lengths were shorter in populations feeding on the introduced species than in populations feeding on the native species, in which the seeds are buried more deeply. The average beak length in museum specimens from each population (indicated by red arrows) was similar to beak lengths in populations feeding on native species.



Conclusion Museum specimens and contemporary data suggest that a change in the seed depth of the soapberry bug's food source can result in evolution by natural selection for a corresponding change in beak size.

Data from S. P. Carroll and C. Boyd, Host race radiation in the soapberry bug: natural history with the history, *Evolution* 46:1052–1069 (1992).

WHAT IF? *Data from additional studies showed that when soapberry bug eggs from a population that fed on balloon vine fruits were then reared on golden rain tree fruits (or vice versa), the beak lengths of the adult insects were most similar to those in the population from which the eggs were initially obtained. Interpret these results.*

length nearly doubled the success with which soapberry bugs could eat the seeds of the introduced species. Furthermore, since historical data show that the golden rain tree reached central Florida just 35 years before the scientific studies were initiated, the results demonstrate that natural selection can cause rapid evolution in a wild population.

The Evolution of Drug-Resistant Bacteria

An example of ongoing natural selection that dramatically affects humans is the evolution of drug-resistant pathogens (disease-causing organisms and viruses). This is a particular problem with bacteria and viruses because they can produce new generations in a short period of time; as a result, resistant strains of these pathogens can proliferate very quickly.

Consider the evolution of drug resistance in the bacterium *Staphylococcus aureus*. About one in three people harbor this species on their skin or in their nasal passages with no negative effects. However, certain genetic varieties (strains) of this species, known as methicillin-resistant *S. aureus* (MRSA), are formidable pathogens. Most MRSA infections are caused by recently appearing strains such as clone USA300, which can cause "flesh-eating disease" and potentially fatal infections **(Figure 22.14)**. How did clone USA300 and other strains of MRSA become so dangerous?

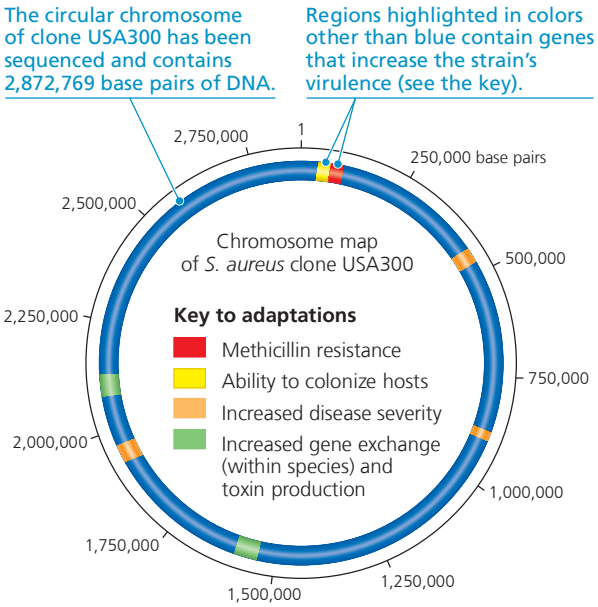
The story begins in 1943, when penicillin became the first widely used antibiotic. Since then, penicillin and other antibiotics have saved millions of lives. However, by 1945, more than 20% of the *S. aureus* strains seen in hospitals were already resistant to penicillin. These bacteria had an enzyme, penicillinase, that could destroy penicillin. Researchers responded by developing antibiotics that were not destroyed by penicillinase, but resistance to each new drug occurred rapidly.

For example, a promising new antibiotic, methicillin, was introduced in 1959. But by 1961, methicillin-resistant strains of *S. aureus* were observed. How did these resistant strains emerge? Methicillin works by deactivating an enzyme that bacteria use to synthesize their cell walls. However, some *S. aureus* populations included individuals that were able to synthesize their cell walls using a different enzyme that was not affected by methicillin. These individuals survived the methicillin treatments and reproduced at higher rates than did other individuals. Over time, these resistant individuals became increasingly common, leading to the spread of MRSA.

Initially, MRSA could be controlled by antibiotics that work differently from the way methicillin works. But this has become less effective because some MRSA strains are resistant to multiple antibiotics—probably because bacteria can exchange genes with members of their own and other species. Thus, the multidrug-resistant strains of today may have emerged over time as MRSA strains that were resistant to different antibiotics exchanged genes.

Finally, it is important to note that *S. aureus* is not the only pathogenic bacterium that has evolved resistance to multiple antibiotics. Furthermore, in recent decades, antibiotic resistance has spread much faster than new antibiotics have been discovered—a problem of great public health concern. Hope may loom on the horizon, however. For example, scientists recently reported the discovery of "teixobactin," a new antibiotic that shows promise for treating MRSA and other pathogens. In addition, as we'll describe in the Scientific Skills Exercise in Chapter 27, the methods used in the discovery of teixobactin may lead to the discovery of other new antibiotics as well.

▼ Figure 22.14 Clone USA300: a virulent strain of methicillin-resistant *Staphylococcus aureus* (MRSA). Resistant to multiple antibiotics and highly contagious, this strain and its close relatives can cause lethal infections of the skin, lungs, and blood. As shown here, researchers have identified key areas of the USA300 genome that code for adaptations that cause its virulent properties.



WHAT IF? *Some drugs being developed specifically target and kill only* S. aureus*; others slow the growth of MRSA but do not kill it. Based on how natural selection works and on the fact that bacterial species can exchange genes, explain why each of these strategies might be effective.*

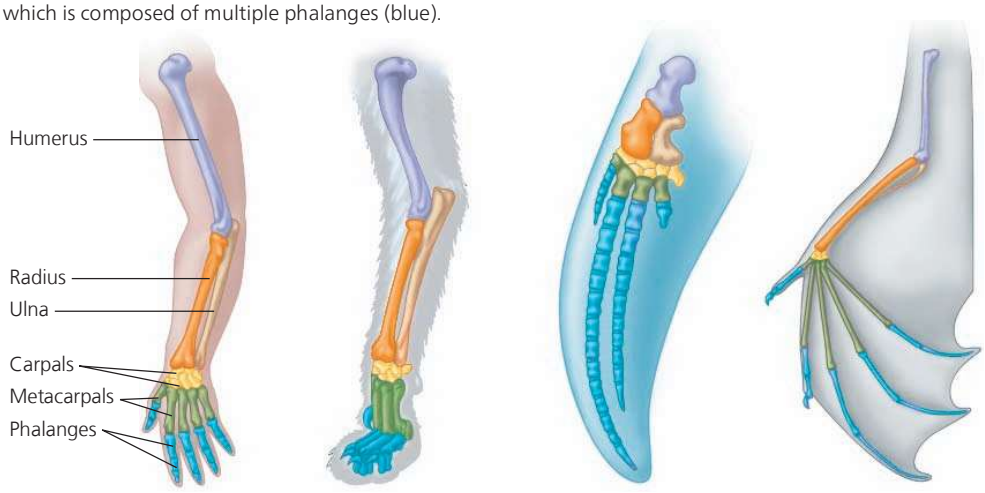
The *S. aureus* and soapberry bug examples highlight three key points about natural selection. First, natural selection is a process of editing, not a creative mechanism. A drug does not *create* resistant pathogens; it *selects for* resistant individuals that are already present in the population. Second, in species that produce new generations in short periods of time, evolution by natural selection can occur rapidly—in just a few years (*S. aureus*) or decades (soapberry bugs). Third, natural selection depends on time and place. It favors those characteristics in a genetically variable population that provide an advantage in the current, local environment. What is beneficial in one situation may be useless or even harmful in another. Beak lengths suitable for the size of the typical fruit eaten by members of a particular soapberry bug population are favored by natural selection. However, a beak length suitable for fruit of one size can be disadvantageous when the bug is feeding on fruit of another size.

Mastering Biology **BBC Video: A Future Without Antibiotics?**

Homology

A second type of evidence for evolution comes from analyzing similarities among different organisms. As we've discussed, evolution is a process of descent with modification: Characteristics present in an ancestral organism are altered (by natural selection) in its descendants over time as they face different environmental conditions. As a result, related species can have characteristics that have an underlying similarity yet function differently. Similarity resulting from common ancestry is known as **homology**. As we'll describe, an understanding of homology can be used to make testable predictions and explain observations that are otherwise puzzling.

▼ Figure 22.15 Mammalian forelimbs: homologous structures. Even though they have become adapted for different functions, the forelimbs of all mammals are constructed from the same basic skeletal elements: one large bone (purple), attached to two smaller bones (orange and tan), attached to several small bones (gold), attached to several metacarpals (green), attached to approximately five digits, each of which is composed of multiple phalanges (blue).



Anatomical and Molecular Homologies

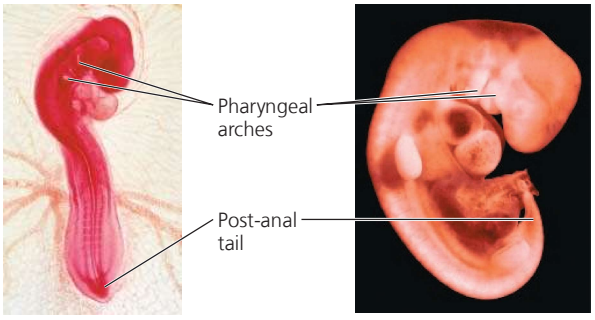
The view of evolution as a remodeling process leads to the prediction that closely related species should share similar features—and they do. Of course, closely related species share the features used to determine their relationship, but they also share many other features. Some of these shared features make little sense except in the context of evolution. For example, the forelimbs of all mammals—including humans, cats, whales, and bats—show the same arrangement of bones from the shoulder to the tips of the digits, even though the appendages have very different functions: lifting, walking, swimming, and flying **(Figure 22.15)**. Such striking anatomical resemblances would be highly unlikely if these structures had arisen anew in each species. Rather, the underlying skeletons of the arms, forelegs, flippers, and wings of different mammals are **homologous structures** that represent variations on a structural theme that was present in their common ancestor.

Comparing early stages of development in different animal species reveals additional anatomical homologies not visible in adult organisms. For example, at some point in their development, all vertebrate embryos have a tail located posterior to (behind) the anus, as well as structures called pharyngeal (throat) arches **(Figure 22.16)**. These homologous arches ultimately develop into structures with very different functions, such as gills in fishes and parts of the ears and throat in humans and other mammals.

Some of the most intriguing homologies concern "leftover" structures of marginal, if any, importance to the organism. These **vestigial structures** are remnants of features that served a function in the organism's ancestors. For instance, snakes arose from ancestors with legs, and the skeletons of some snakes retain vestiges of the pelvis and leg bones of their ancestors. Likewise, blind species of cave fishes descended from ancestors with eyes—which explains why these blind fishes have eye remnants buried under their scales. We would not expect to see these vestigial structures if snakes and blind cave fishes had origins separate from those of other vertebrate animals.

Biologists also observe similarities among organisms at the molecular level. All forms of life use essentially the same genetic code, suggesting that all species descended from common ancestors that used this code. But molecular homologies go beyond a shared code. For example, organisms as dissimilar as humans and bacteria share genes inherited from a very distant common ancestor. Some of these homologous genes

▼ Figure 22.16 Anatomical similarities in vertebrate embryos. At some stage in their embryonic development, all vertebrates have a tail located posterior to the anus (referred to as a post-anal tail), as well as pharyngeal (throat) arches. Descent from a common ancestor can explain such similarities.



have acquired new functions, while others, such as those coding for the ribosomal subunits used in protein synthesis (see Figure 17.18), have retained their original functions. It is also common for organisms to have genes that have lost their function, even though the homologous genes in related species may be fully functional. Like vestigial structures, it appears that such inactive "pseudogenes" may be present simply because a common ancestor had them.

Homologies and "Tree Thinking"

Some homologous characteristics, such as the genetic code, are shared by all species because they date to the deep ancestral past. In contrast, homologous characteristics that evolved more recently are shared only within smaller groups of organisms.

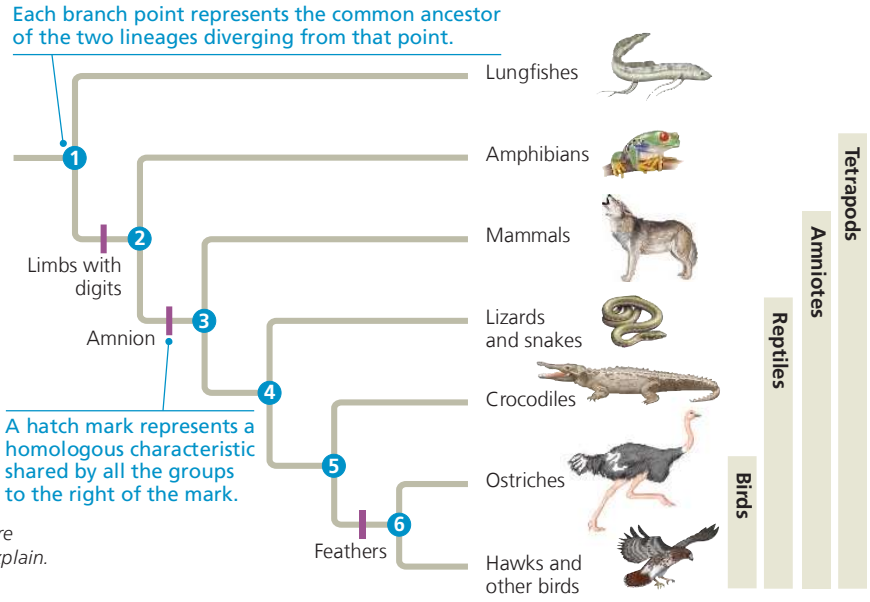
Consider the *tetrapods* (from the Greek *tetra*, four, and *pod*, foot), the vertebrate group that consists of amphibians, mammals, and reptiles. Like all vertebrates, tetrapods have a backbone. But unlike other vertebrates, tetrapods also have limbs with digits (see Figure 22.15). As suggested by this example, homologous characteristics form a nested pattern: All life shares the deepest layer (in this case, all vertebrates have a backbone), and each successive smaller group adds its own homologies to those it shares with larger groups (in this case, all tetrapods have a backbone *and* limbs with digits). This nested pattern is exactly what we would expect to result from descent with modification from a common ancestor.

Biologists often represent the pattern of descent from common ancestors with an **evolutionary tree**, a diagram that reflects evolutionary relationships among groups of organisms. We will explore evolutionary trees in more detail in Chapter 26, but for now, let's consider how we can interpret and use such trees.

Figure 22.17 is an evolutionary tree of tetrapods and their closest living relatives, the lungfishes. In this diagram, each branch point represents the most recent common ancestor of the two lineages diverging from that point. For example, lungfishes and all tetrapods descended from ancestor 1, whereas mammals, lizards and snakes, crocodiles, and birds all descended from ancestor 3. As expected, the three homologies shown on the tree—limbs with digits, the amnion (a protective embryonic membrane), and feathers—form a nested pattern. Limbs with digits were present in common ancestor 2 and hence are found in all of the descendants of that ancestor (the tetrapods). The amnion was present only in ancestor 3 and hence is shared only by some tetrapods (mammals and reptiles). Feathers were present only in ancestor 6 and hence are found only in birds.

To explore "tree thinking" further, note that in Figure 22.17 mammals are positioned closer to amphibians than to birds. As a result, you might conclude that mammals are more closely related to amphibians than they are to birds. However, mammals are actually more closely related to birds than to amphibians because mammals and birds share a more recent common ancestor (ancestor 3) than do mammals and amphibians (ancestor 2). Ancestor 2 is also the most recent common ancestor of birds and amphibians, making mammals and birds equally related to amphibians. Finally, note that the tree in Figure 22.17 shows the relative timing of events but not their actual dates. Thus, we can conclude that ancestor 2 lived before ancestor 3, but we do not know when that was.

Evolutionary trees are hypotheses that summarize our current understanding of patterns of descent. Our confidence in these relationships, as with any hypothesis, depends on the strength of the supporting data. In the case of Figure 22.17, the tree is supported by many different data sets, including both anatomical and DNA sequence data. As a result, biologists are confident that it accurately reflects evolutionary history. Scientists can use such well-supported evolutionary trees to make specific and sometimes surprising predictions about organisms (see Figure 26.17).



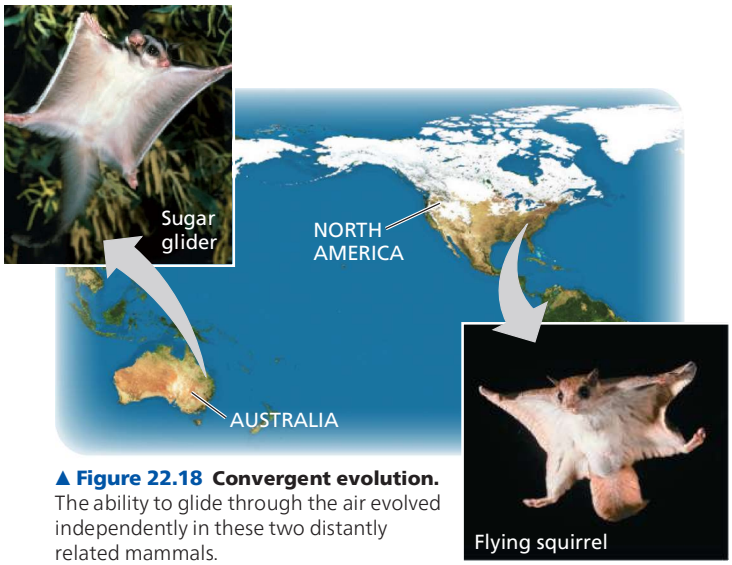
▶ Figure 22.17 Tree thinking: information provided in an evolutionary tree. This evolutionary tree for tetrapods and their closest living relatives, the lungfishes, is based on anatomical and DNA sequence data. The purple hatch marks indicate the origin of three important homologies, each of which evolved only once. Birds are nested within and evolved from reptiles; hence, the group of organisms called "reptiles" technically includes birds.

VISUAL SKILLS *Based on this evolutionary tree, are crocodiles more closely related to lizards or birds? Explain.*

Mastering Biology Figure Walkthrough

A Different Cause of Resemblance: Convergent Evolution

Although organisms that are closely related share characteristics because of common descent, distantly related organisms can resemble one another for a different reason: **convergent evolution**, the independent evolution of similar features in different lineages. Consider marsupial mammals, many of which live in Australia. Marsupials are distinct from another group of mammals—the eutherians, or placental mammals—few of which live in Australia. (Eutherians complete their embryonic development in the uterus, whereas marsupials are born as embryos and complete their development while nursing, often in an external pouch.) Some Australian marsupials have eutherian look-alikes with superficially similar adaptations. For instance, a forest-dwelling Australian marsupial called the sugar glider is superficially very similar to flying squirrels, gliding eutherians that live in North American forests **(Figure 22.18)**. But the sugar glider has many other characteristics that make it a marsupial, much more closely related to kangaroos and other Australian marsupials than to flying squirrels or other eutherians. Once again, our understanding of evolution can explain these observations. Although they evolved independently from different ancestors, these two mammals have adapted to similar environments in similar ways. In such examples in which species share features because of convergent evolution, the resemblance is said to be **analogous**, not homologous. Analogous features share similar function, but not common ancestry, while homologous features share common ancestry, but not necessarily similar function.



▲ Figure 22.18 Convergent evolution. The ability to glide through the air evolved independently in these two distantly related mammals.

The Fossil Record

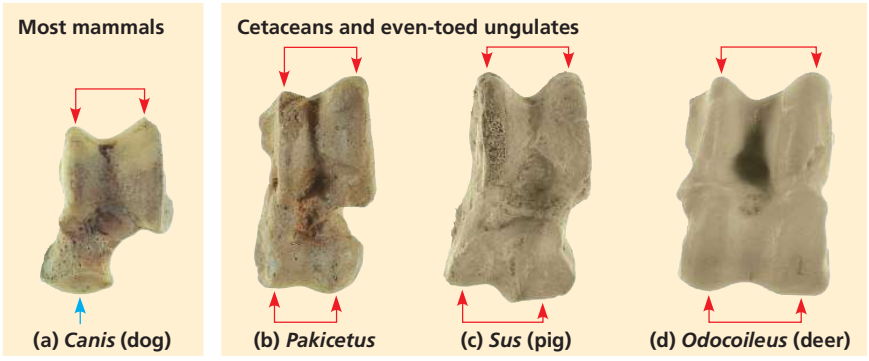
A third type of evidence for evolution comes from fossils. The fossil record documents the pattern of evolution, showing that past organisms differed from present-day organisms and that many species have become extinct. Fossils also show the evolutionary changes that have occurred in various groups of organisms. To give one of hundreds of possible examples, researchers found that over several thousand years, the pelvic bone in fossil stickleback fish became greatly reduced in size. The consistent nature of this change over time suggests that the reduction in the size of the pelvic bone may have been driven by natural selection.

Fossils can also shed light on the origins of new groups of organisms. An example is the fossil record of cetaceans, the mammalian order that includes whales, dolphins, and porpoises. Some of these fossils **(Figure 22.19)** provided strong support for a hypothesis based on DNA sequence data: that cetaceans are closely related to even-toed ungulates, a group that includes hippopotamuses, pigs, deer, and cows.

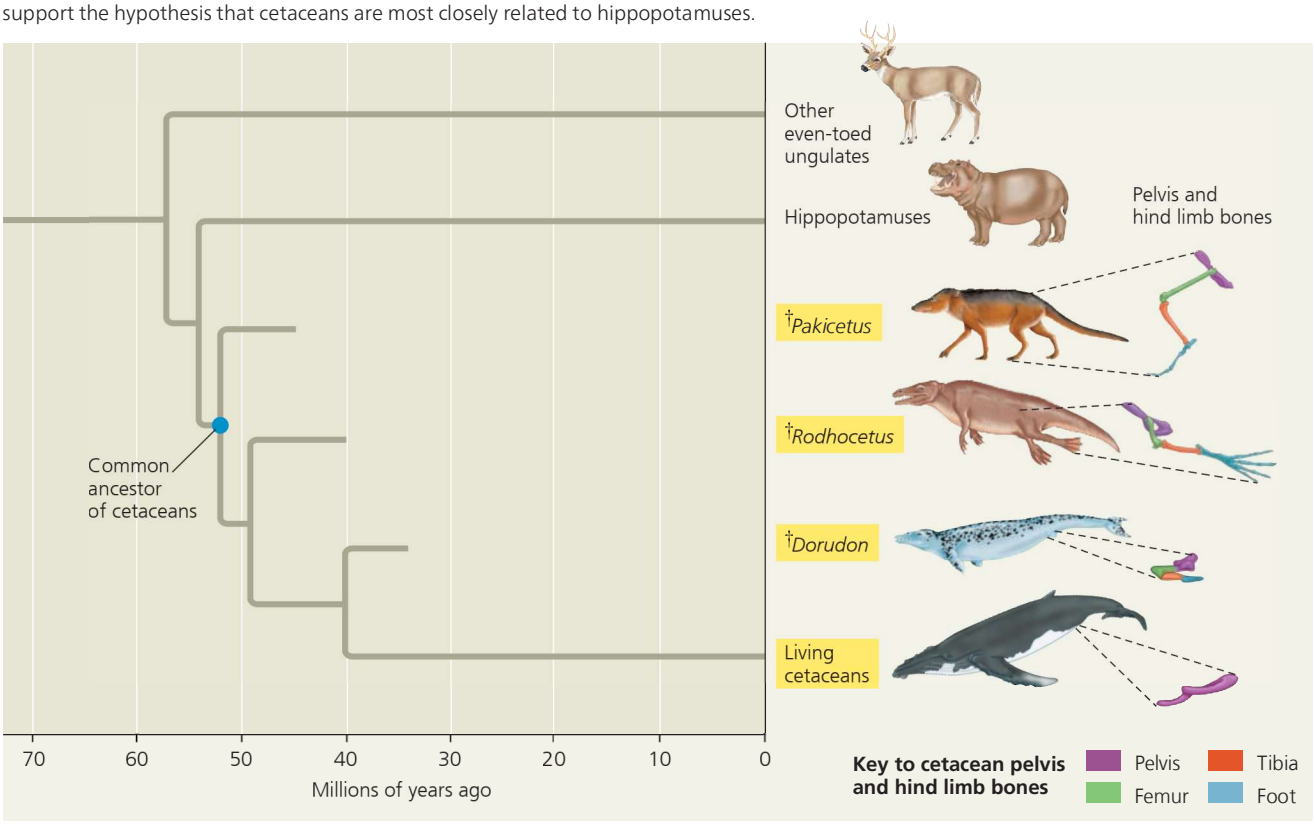
What else can fossils tell us about cetacean origins? The earliest cetaceans lived 50–60 million years ago. The fossil record indicates that prior to that time, most mammals were terrestrial. Although scientists had long realized that whales and other cetaceans originated from land mammals, few fossils had been found that revealed how cetacean limb structure had changed over time, leading eventually to the development of flippers as well as to the loss of hind limbs and the development of flukes (the lobes on a whale's tail). In the past few decades, however, a series of remarkable fossils have been discovered in Pakistan, Egypt, and North America. These fossils document steps in the transition from life on land to life in the sea, filling in some of the gaps between ancestral and living cetaceans **(Figure 22.20)**.

Finally, although living cetaceans look very different from living even-toed ungulates, the fossil discoveries show that extinct early cetaceans such as *Pakicetus* looked fairly similar

▼ Figure 22.19 Ankle bones: one piece of the puzzle. Comparing fossils and present-day examples of the astragalus (a type of ankle bone) indicates that cetaceans are closely related to even-toed ungulates. **(a)** In most mammals, the astragalus is shaped like that of a dog, with a double hump on one end (red arrows) but not at the opposite end (blue arrow). **(b)** Fossils show that the early cetacean *Pakicetus* had an astragalus with double humps at both ends, a shape otherwise found only in pigs **(c)**, deer **(d)**, and all other even-toed ungulates.



▼ Figure 22.20 The transition to life in the sea. Multiple lines of evidence support the hypothesis that cetaceans (yellow labels) evolved from terrestrial mammals. Fossils document the reduction over time in the pelvis and hind limb bones of extinct (†) cetacean ancestors, including *Pakicetus, Rodhocetus,* and *Dorudon*. DNA sequence data support the hypothesis that cetaceans are most closely related to hippopotamuses.

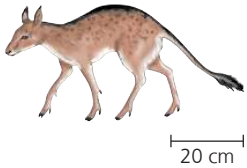


VISUAL SKILLS *Use the diagram to determine which happened first during the evolution of cetaceans: changes in hind limb structure or the origin of tail flukes (the lobes on a whale's tail). Explain.*

Mastering Biology Figure Walkthrough

to deer and other living even-toed ungulates. The extinct early cetaceans also looked very similar to extinct early even-toed ungulates, such as *Diacodexis* **(Figure 22.19)**. Similar patterns are seen in fossils documenting the origins of other groups of organisms, including mammals (see Figure 25.7), flowering plants (see Concept 30.3), and tetrapods (see Figure 34.21). In each of these cases, the fossil record shows that over time, descent with modification produced increasingly large differences among related groups of organisms, ultimately resulting in the diversity of life today.

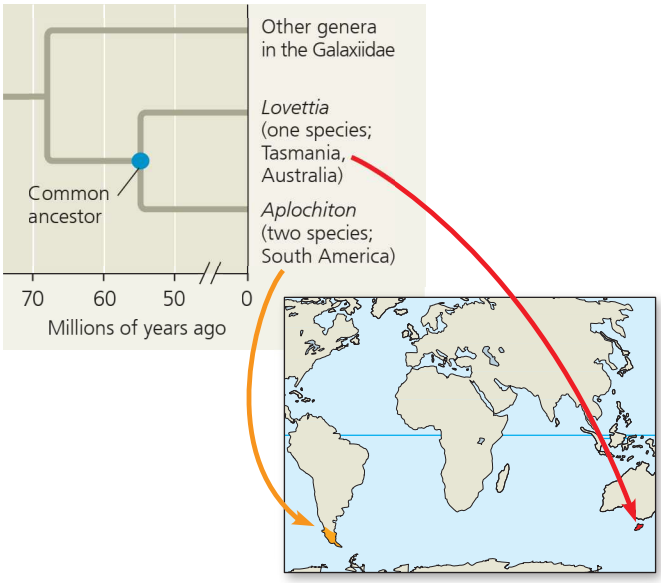
▼ Figure 22.21 *Diacodexis*, an early even-toed ungulate.



Biogeography

A fourth type of evidence comes from **biogeography**, the scientific study of the geographic distributions of species. These distributions are influenced by many factors, including *continental drift*, the slow movement of Earth's continents over time. About 250 million years ago, these movements united all of Earth's landmasses into a single large continent called **Pangaea**

▼ Figure 22.22 Closely related freshwater fish separated by 9,000 km of ocean. There are three species in these two closely related genera of freshwater fish within the family Galaxiidae.



(see Figure 25.16). Roughly 200 million years ago, Pangaea began to break apart; by 20 million years ago, the continents were within a few hundred kilometers of their present locations.

We can use our understanding of evolution and continental drift to predict where fossils of different groups of organisms might be found. For example, scientists have constructed evolutionary trees for horses based on anatomical data. These trees and the ages of fossils of horse ancestors suggest that the genus that includes present-day horses (*Equus*) originated 5 million years ago in North America. Geologic evidence indicates that at that time, North and South America were not yet connected, making it difficult for horses to travel between them. Thus, we would predict that the oldest *Equus* fossils should be found only on the continent on which the group originated—North America. This prediction and others like it for different groups of organisms have been upheld, providing more evidence for evolution.

Evolution also explains biogeographic data. For example, a group of three species of freshwater fish in the family Galaxiidae are found in regions separated by wide stretches of open ocean **(Figure 22.22)**. None of these three species can survive in salt water, so how can we explain their geographic distributions? These three species represent all known living descendants of a common ancestor. Since all of the living species cannot survive in salt water, it is likely that their common ancestor also was restricted to freshwater habitats. At first glance, this only deepens the mystery—how could that ancestor or its descendants have swum across vast stretches of ocean? A clue comes from genetic analyses indicating that the evolutionary lineages leading to these three species began to diverge about 55 million years ago. By that time, the southernmost portion of Pangaea was breaking apart into what would eventually become South America, Australia, and Antarctica. This suggests that their ancestors had spread across southern Pangaea before it broke apart. At later times, these three freshwater species originated on the continental regions where they currently live, resulting in their present-day geographic distribution.

What Is Theoretical About Darwin's View of Life?

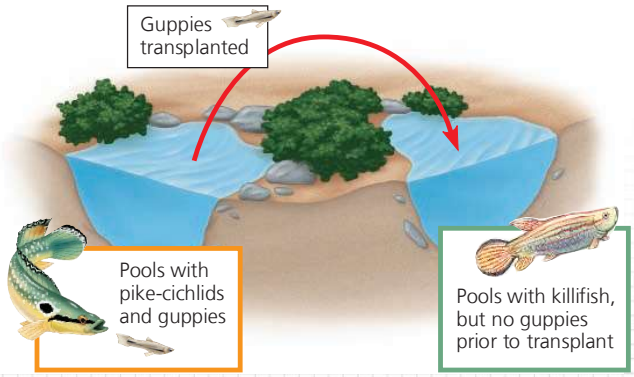
Some people dismiss Darwin's ideas as "just a theory." But the *pattern* of evolution—the observation that life has evolved

Scientific Skills Exercise

Making and Testing Predictions

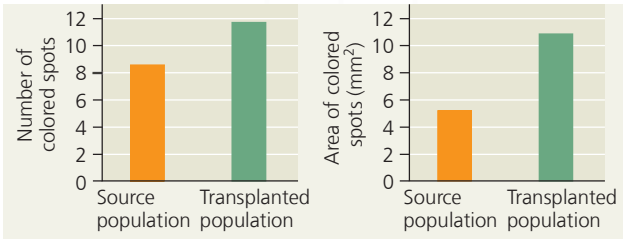
Can Predation Result in Natural Selection for Color Patterns in Guppies? Our understanding of evolution changes constantly as new observations lead to new hypotheses—and hence to new ways to test our understanding of evolutionary theory. Consider the wild guppies (*Poecilia reticulata*) that live in pools connected by streams on the Caribbean island of Trinidad. Male guppies have highly varied color patterns that are controlled by genes that are only expressed in adult males. Female guppies choose males with bright color patterns as mates more often than they choose males with drab coloring. But the bright colors that attract females also can make the males more conspicuous to predators. Researchers observed that in pools with few predator species, the benefits of bright colors appear to "win out," and males are more brightly colored than in pools where predation is more intense.

One guppy predator, the killifish, preys on juvenile guppies that have not yet displayed their adult coloration. Researchers predicted that if adult guppies with drab colors were transferred to a pool with only killifish, eventually the descendants of these guppies would be more brightly colored (because of the female preference for brightly colored males).



How the Experiment Was Done Researchers transplanted 200 adult guppies from pools containing pike-cichlid fish, predators of adult guppies, to pools with only killifish, predators of juvenile guppies. They tracked the number of bright-colored spots and the total area of those spots on adult male guppies in each generation.

Data from the Experiment After 22 months (15 generations), researchers compared the color pattern data for guppies from the source and transplanted populations.



Data from J. A. Endler, Natural selection on color patterns in *Poecilia reticulata*, *Evolution* 34:76–91 (1980).

INTERPRET THE DATA

1. Identify the following elements of hypothesis-based science in this example: **(a)** question, **(b)** hypothesis, **(c)** prediction, **(d)** control group, and **(e)** experimental group. (For additional information about hypothesis-based science, see Concept 1.3 and the Scientific Skills Review in Appendix D.)
2. Explain how the types of data the researchers chose to collect enabled them to test their prediction.
3. What conclusion do you draw from the data presented above?
4. **(a)** Predict what would happen if, after 22 months, guppies from the transplanted population were returned to the source pool. **(b)** Describe an experiment to test your prediction.

Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

over time—is supported by a great deal of evidence. In addition, Darwin's explanation of the *process* of evolution—that natural selection is the primary cause of the observed pattern of evolutionary change—makes sense of massive amounts of data. As the **Scientific Skills Exercise** describes, the effects of natural selection also can be observed and tested in nature.

What, then, is theoretical about evolution? Keep in mind that the scientific meaning of the term *theory* is very different from its meaning in everyday use. The colloquial use of the word *theory* comes close to what scientists mean by a hypothesis. In science, a theory is much more comprehensive than a hypothesis. A theory, such as the theory of evolution by natural selection, accounts for many observations and explains and integrates a great variety of phenomena. Such a unifying theory does not become widely accepted unless its predictions stand up to thorough and continual testing by experiment and additional observation (see Concept 1.3). As the rest of this unit demonstrates, this has certainly been the case with the theory of evolution by natural selection.

The skepticism of scientists as they continue to test theories prevents these ideas from becoming dogma. For example, although Darwin thought that evolution was a very slow process, we now know that this isn't always true. Populations can evolve rapidly, and new species can form in relatively short periods of time: a few thousand years or less. Furthermore, evolutionary biologists now recognize that natural selection is not the only mechanism responsible for evolution. Indeed, the study of evolution today is livelier than ever as scientists use a wide range of experimental approaches and genetic analyses to test predictions based on natural selection and other evolutionary mechanisms.

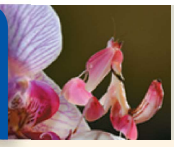
Although Darwin's theory attributes life's diversity to natural processes, the diverse products of evolution are nevertheless elegant and inspiring. As Darwin wrote in the final sentence of *The Origin of Species*, "There is grandeur in this view of life . . . [in which] endless forms most beautiful and most wonderful have been, and are being, evolved."

CONCEPT CHECK 22.3

1. Explain how the following statement is inaccurate: "Antibiotics have created drug resistance in MRSA."
2. How does evolution account for (a) the similar mammalian forelimbs with different functions shown in Figure 22.15 and (b) the similar forms of the two distantly related mammals shown in Figure 22.18?
3. **WHAT IF?** Fossils show that dinosaurs originated 200–250 million years ago. Would you expect the geographic distribution of early dinosaur fossils to be broad (on many continents) or narrow (on one or a few continents only)? Explain.

For suggested answers, see Appendix A.

22 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

CONCEPT 22.1

The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species *(pp. 469–471)*

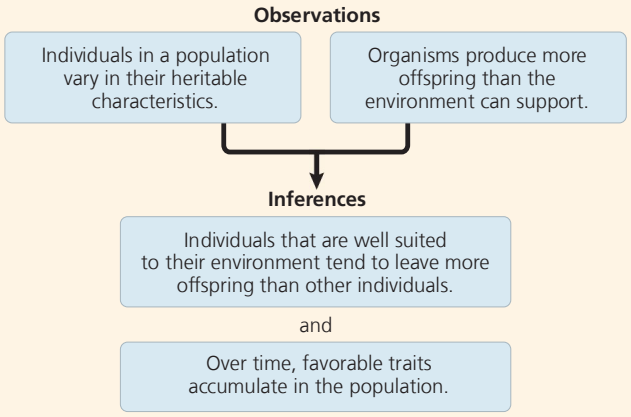
- Darwin proposed that life's diversity arose over long periods of time from ancestral species through natural selection, a departure from prevailing views. For example, Cuvier studied **fossils** but denied that **evolution** occurs; he proposed that sudden catastrophic events in the past caused species to disappear from an area. Lamarck hypothesized that species evolve, but the underlying mechanisms he proposed are not supported by evidence.

? *Why was the age of Earth important for Darwin's ideas about evolution?*

CONCEPT 22.2

Descent with modification by natural selection explains the adaptations of organisms and the unity and diversity of life *(pp. 471–476)*

- Darwin's experiences during the voyage of the *Beagle* gave rise to his idea that new species originate from ancestral forms through the accumulation of **adaptations**. He refined his theory for many years and finally published it in 1859 after learning that Wallace had come to the same idea.
- In *The Origin of Species*, Darwin proposed that over long periods of time, descent with modification produced the rich diversity of life through the mechanism of **natural selection**.



? *Describe how overreproduction and heritable variation relate to evolution by natural selection.*

CONCEPT 22.3

Evolution is supported by an overwhelming amount of scientific evidence *(pp. 476–484)*

- Researchers have directly observed natural selection leading to evolution in many studies in diverse organisms.
- Organisms share characteristics because of common descent (**homology**) or because natural selection affects independently evolving species in similar environments in similar ways (**convergent evolution**).
- Fossils show that past organisms differed from living organisms, that many species have become extinct, and that species have evolved over long periods of time; fossils also document the evolutionary origin of new groups of organisms.
- Evolutionary theory can explain some **biogeographic** patterns.

? *Summarize the different lines of evidence supporting the hypothesis that cetaceans descended from land mammals and are closely related to even-toed ungulates.*

TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the Mastering Biology eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

1. Which of the following is an observation or inference on which natural selection is based?
   (A) Individuals do not vary in their heritable characteristics.
   (B) Only well-adapted individuals produce offspring.
   (C) Species produce more offspring than the environment can support.
   (D) Nearly all of each individual's offspring will survive and reproduce.
2. Which of the following observations helped Darwin shape his concept of descent with modification?
   (A) Species diversity declines farther from the equator.
   (B) Fewer species live on islands than on the nearest continents.
   (C) Birds live on islands located farther from the mainland than the birds' maximum nonstop flight distance.
   (D) South American temperate plants are more similar to South American tropical plants than to European temperate ones.

Levels 3-4: Applying/Analyzing

3. Within six months of effectively using methicillin to treat *S. aureus* infections in a community, all new *S. aureus* infections were caused by a resistant strain (MRSA). How can this best be explained?
   (A) A patient must have become infected with MRSA from another community.
   (B) In response to the drug, *S. aureus* began making drug-resistant versions of the protein targeted by the drug.
   (C) Some drug-resistant bacteria were present at the start of treatment, and natural selection increased their frequency.
   (D) *S. aureus* evolved to resist vaccines.
4. DNA sequences in many human genes are very similar to the sequences of corresponding genes in chimpanzees. The most likely explanation for this result is that
   (A) humans and chimpanzees share a relatively recent common ancestor.
   (B) humans evolved from chimpanzees.
   (C) chimpanzees evolved from humans.
   (D) convergent evolution led to the DNA similarities.
5. The upper forelimbs of humans and bats have fairly similar skeletal structures, whereas the corresponding bones in whales have very different shapes and proportions. However, genetic data suggest that all three kinds of organisms diverged from a common ancestor at about the same time. Which of the following is the most likely explanation for these data?
   (A) Forelimb evolution was adaptive in people and bats, but not in whales.
   (B) Natural selection in an aquatic environment resulted in significant changes to whale forelimb anatomy.
   (C) Genes mutate faster in bats than in humans or whales.
   (D) Whales are not properly classified as mammals.

Levels 5-6: Evaluating/Creating

6. **EVOLUTION CONNECTION** Explain why anatomical and molecular features often fit a similar nested pattern. In addition, describe a process that can cause this not to be the case.
7. **SCIENTIFIC INQUIRY • DRAW IT** Mosquitoes resistant to the pesticide DDT first appeared in India in 1959, but now are found throughout the world. (a) Graph the data in the table below. (b) After examining the graph, hypothesize why the percentage of mosquitoes resistant to DDT rose rapidly. (c) Suggest an explanation for the global spread of DDT resistance.

Month	0	8	12
Mosquitoes Resistant* to DDT	4%	45%	77%

*Mosquitoes were considered resistant if they were not killed within 1 hour of receiving a dose of 4% DDT.

Data from C. F. Curtis et al., Selection for and against insecticide resistance and possible methods of inhibiting the evolution of resistance in mosquitoes, *Ecological Entomology* 3:273–287 (1978).

8. **WRITE ABOUT A THEME: INTERACTIONS** Write a short essay (about 100–150 words) evaluating whether changes to an organism's physical environment are likely to result in evolutionary change. Use an example to support your reasoning.
9. **SYNTHESIZE YOUR KNOWLEDGE**



This honeypot ant (genus *Myrmecocystus*) can store liquid food inside its expandable abdomen. Consider other ants you are familiar with, and explain how a honeypot ant exemplifies three key features of life: adaptation, unity, and diversity.

For selected answers, see Appendix A.

Explore Scientific Papers with Science in the Classroom AAAS
How are some coral reefs responding to climate change?
Go to "Take the Heat" at
www.scienceintheclassroom.org.
Instructors: Questions can be assigned in Mastering Biology.

23 The Evolution of Populations

KEY CONCEPTS

23.1 **Genetic variation makes evolution possible** *p. 487*

23.2 **The Hardy-Weinberg equation can be used to test whether a population is evolving** *p. 489*

23.3 **Natural selection, genetic drift, and gene flow can alter allele frequencies in a population** *p. 493*

23.4 **Natural selection is the only mechanism that consistently causes adaptive evolution** *p. 497*

Study Tip

Make a table: This chapter discusses different types of selection—disruptive, stabilizing, sexual, balancing, frequency-dependent, and heterozygote advantage. These types of selection are not all mutually exclusive, and some evolutionary changes are examples of more than one. To help you study, make a table like the one shown listing each type of selection, its distinguishing features, and example(s) from the chapter.

Type of selection	Distinguishing features	Example
Balancing selection	Maintains two or more phenotypes in a population; includes frequency-dependent selection and heterozygote advantage	Figures 23.17 and 23.18
Directional selection		

Go to Mastering Biology

For Students (in eText and Study Area)
- Get Ready for Chapter 23
- Figure 23.8 Walkthrough: Hardy-Weinberg Equilibrium
- BioFlix® Animation: Natural Selection, Genetic Drift, and Gene Flow

For Instructors to Assign (in Item Library)
- Tutorial: The Hardy-Weinberg Principle

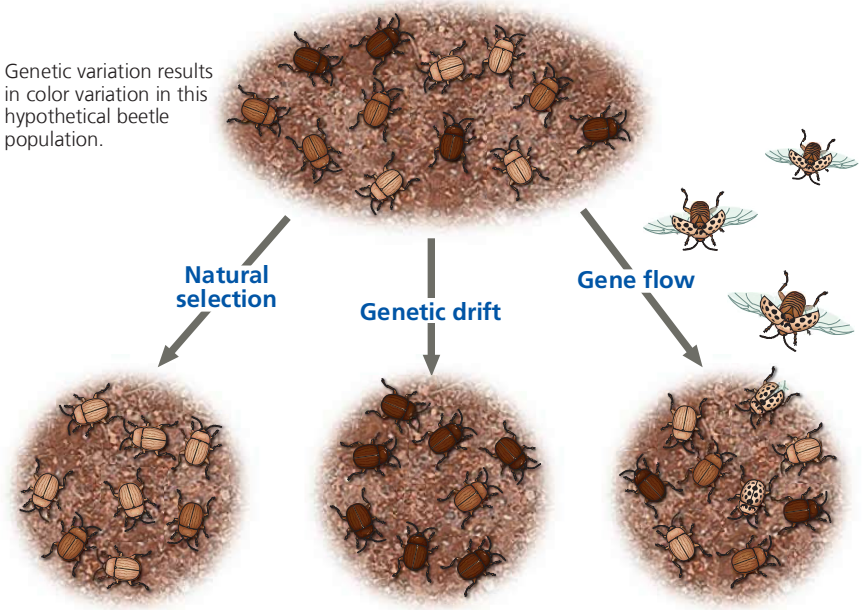
Ready-to-Go Teaching Module (in Instructor Resources)
- Mechanisms of Evolution



Figure 23.1 The medium ground finch (*Geospiza fortis*) is a seed-eating bird that inhabits the Galápagos Islands. In 1977, the *G. fortis* population on the island of Daphne Major was decimated by a long period of drought: Of some 1,200 birds, only 180 survived. The surviving birds had larger, deeper beaks, indicating that this population of finches had evolved.

What mechanisms can cause the evolution of populations?

Evolution occurs when natural selection, genetic drift, or gene flow alter the allele frequencies of a population over time.



A common misconception about evolution is that individual organisms evolve. It is true that natural selection acts on individuals: Each organism's traits affect its survival and reproductive success compared with other individuals. But the impact of natural selection only becomes apparent in how a *population* of organisms changes over time.

To see why, consider the population of medium ground finches decimated by a drought, resulting in only 180 survivors out of some 1,200 birds. Researchers Peter and Rosemary Grant observed that during the drought, small, soft seeds were scarce, while large, hard seeds were more plentiful. Birds with larger, deeper beaks were better able to crack and eat the larger seeds and survived at a higher rate than finches with smaller beaks.

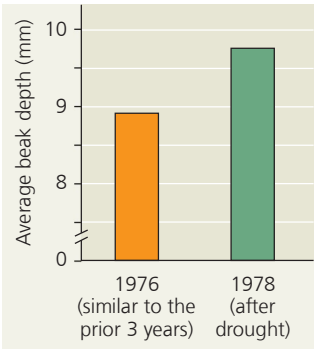
Since beak depth is an inherited trait in these birds, the offspring of surviving birds also tended to have deep beaks. As a result, the average beak depth in the next generation of *G. fortis* was greater than it had been in the pre-drought population **(Figure 23.2)**. The finch population had evolved by natural selection. However, the *individual* finches did not evolve. Each bird had a beak of a particular size, which did not grow larger during the drought. Rather, the proportion of large beaks in the population increased from generation to generation: The population evolved, not its individual members.

Focusing on evolutionary change in populations, we can define evolution on its smallest scale, called **microevolution**, as a change in allele frequencies in a population over generations. In the finch population, for example, birds that had alleles encoding large beaks survived at higher rates than did other birds—causing those alleles to be more common after the drought than they had been before it. There are three main mechanisms that can cause such changes in allele frequencies: natural selection, genetic drift (chance events that alter allele frequencies), and gene flow (the transfer of alleles between populations). Each of these mechanisms affects the genetic composition of populations, but only natural selection consistently improves the degree to which organisms are well suited for life in their environment (adaptation). Before we examine this more closely, let's revisit a prerequisite for these processes: genetic variation.

Mastering Biology
Interview with Rosemary and Peter Grant: Studying evolution in the Galápagos finches



▶ Figure 23.2 Evidence of selection by food source. The data represent adult beak depths of finches hatched before and after the 1977 drought. In one generation, natural selection resulted in a larger average beak size in the population.



Instructors: A related Experimental Inquiry Tutorial can be assigned in **Mastering Biology**.

CONCEPT 23.1

Genetic variation makes evolution possible

In *The Origin of Species*, Darwin provided abundant evidence that life on Earth has evolved over time, and he proposed natural selection as the primary mechanism for that change. He observed that individuals differ in their inherited traits and that selection acts on such differences, leading to evolutionary change. Although Darwin realized that variation in heritable traits is a prerequisite for evolution, he did not know precisely how organisms pass heritable traits to their offspring.

Just a few years after Darwin published *The Origin of Species*, Gregor Mendel wrote a groundbreaking paper on inheritance in pea plants proposing a model of inheritance in which organisms transmit discrete heritable units (now called genes) to their offspring. Although Darwin did not know about genes, Mendel's paper set the stage for understanding the genetic differences on which evolution is based.

Genetic Variation

Individuals within all species vary in their phenotypic traits. Humans, for example, vary noticeably in facial features, height, and voice. And though you cannot identify blood group (A, B, AB, or O) from a person's appearance, this and many other molecular traits also vary extensively among individuals.

Such phenotypic variations often reflect **genetic variation**, differences among individuals in the composition of their genes or other DNA sequences. Some heritable phenotypic differences occur on an "either-or" basis, such as the flower colors of Mendel's pea plants: Each plant had flowers that were either purple or white (see Figure 14.3). Characters that vary in this way are typically determined by a single gene locus, with different alleles producing distinct phenotypes. In contrast, other phenotypic differences vary in gradations along a continuum. Such variation usually results from the influence of two or more genes on a single phenotypic character. In fact, many phenotypic characters are influenced by multiple genes, including coat color in horses **(Figure 23.3)**, seed number in maize (corn), and height in humans.

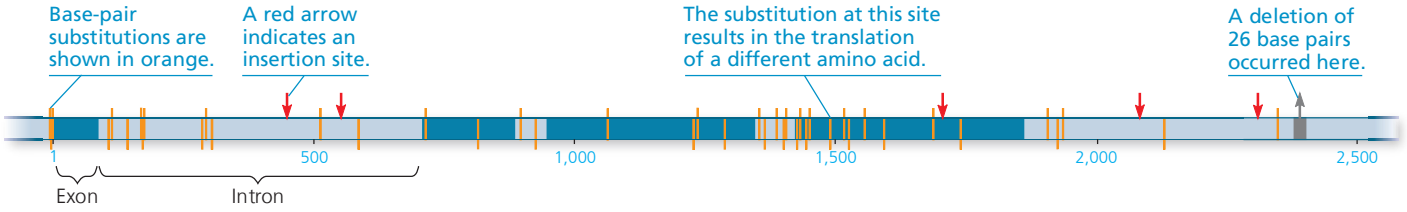
How much do genes and other DNA sequences vary from one individual to another? Genetic variation at the

▼ Figure 23.3 Phenotypic variation in horses.



▼ Figure 23.4 Extensive genetic variation at the molecular level. This diagram summarizes data from a study comparing the DNA sequence of the alcohol dehydrogenase (*Adh*) gene in several fruit flies (*Drosophila melanogaster*). The *Adh* gene has four exons (dark blue) separated by introns (light blue); the exons include the coding regions that are ultimately translated into the amino acids of the Adh enzyme (see Figure 5.1). Only one substitution has a phenotypic effect, producing a different form of the Adh enzyme.

MAKE CONNECTIONS *Review Figures 17.6 and 17.11. Explain how a base-pair substitution that alters a coding region of the* Adh *locus could have no effect on amino acid sequence. Then explain how an insertion in an exon could have no effect on the protein produced.*



whole-gene level (*gene variability*) can be quantified as the average percentage of loci that are heterozygous. (Recall that a heterozygous individual has two different alleles for a given locus, whereas a homozygous individual has two identical alleles for that locus.) As an example, on average the fruit fly *Drosophila melanogaster* is heterozygous for about 1,920 of its 13,700 loci (14%) and homozygous for all the rest.

Considerable genetic variation can also be measured at the molecular level of DNA (*nucleotide variability*). But little of this variation results in phenotypic variation. Why? Many nucleotide variations occur within *introns*, noncoding segments of DNA lying between *exons*, the regions retained in mRNA after RNA processing (see Figure 17.12). And of the variations that occur within exons, most do not cause a change in the amino acid sequence of the protein encoded by the gene. For example, in the sequence comparison shown in **Figure 23.4**, there are 43 nucleotide sites with variable base pairs (where substitutions have occurred), as well as several sites where insertions or deletions have occurred. Although 18 variable sites occur within the four exons of the *Adh* gene, only one of these variations (at site 1,490) results in an amino acid change. Note, however, that this single variable site is enough to cause genetic variation at the level of the gene, and hence two different forms of the Adh enzyme are produced.

It is important to bear in mind that some phenotypic variation does not result from genetic differences among individuals (**Figure 23.5** shows a striking example in a caterpillar of the southwestern United States). Phenotype is the product of an inherited genotype and many environmental influences (see Concept 14.3). In a human example, bodybuilders alter their phenotypes dramatically but do not pass their huge muscles on to the next generation. In general, only the genetically determined part of phenotypic variation can have evolutionary consequences. As such, genetic variation provides the raw material for evolutionary change: *Without genetic variation, evolution cannot occur.*

Sources of Genetic Variation

Genetic variation originates when mutation, gene duplication, or other processes produce new alleles and new genes. Genetic variants can be produced rapidly in organisms with short generation times. Sexual reproduction can also result in genetic variation as existing genes are arranged in new ways.

Formation of New Alleles

New alleles can arise by *mutation*, a change in the nucleotide sequence of an organism's DNA. Mutations can be caused by factors such as errors in DNA replication, exposure to UV light and other high-energy forms of radiation, and exposure to certain chemicals (see Concept 17.5). A change of as little as one base in a gene—a "point mutation"—can have a significant impact on phenotype, as in sickle-cell disease (see Figure 23.18). Furthermore, organisms reflect many generations of past selection, and hence their phenotypes tend to be well suited for life in their environments. As a result, most new mutations that alter a phenotype are at least slightly harmful.

In some cases, natural selection quickly removes such harmful alleles. In diploid organisms, however, harmful alleles that are recessive can be hidden from selection. Indeed, a harmful recessive allele can persist for generations by propagation in heterozygous individuals (where its harmful effects can be masked by the more favorable dominant allele). Such "heterozygote protection" maintains a huge pool of alleles

▼ Figure 23.5 Nonheritable variation. These caterpillars of the moth *Nemoria arizonaria* owe their different appearances to chemicals in their diets, not to differences in their genotypes. **(a)** Caterpillars raised on a diet of oak flowers resemble the flowers, whereas **(b)** their siblings raised on oak leaves resemble oak twigs.





that may be harmful under present conditions, but that could be beneficial if the environment changes.

While many mutations are harmful, many others are not. Recall that much of the DNA in eukaryotic genomes does not encode proteins (see Figure 21.6). Point mutations in these noncoding regions generally result in **neutral variation**, differences in DNA sequence that do not confer a selective advantage or disadvantage. The redundancy in the genetic code is another source of neutral variation: Even a point mutation in a gene that encodes a protein will have no effect on the protein's function if the amino acid doesn't change. And even a change in the amino acid may not affect the protein's shape and function. Moreover, a mutant allele may on rare occasions actually make its bearer better suited to the environment, enhancing reproductive success.

Finally, note that in multicellular organisms, only mutations in cell lines that produce gametes can be passed to offspring. In plants and fungi, this is not as limiting as it may sound, since many different cell lines can produce gametes. But in most animals, the majority of mutations occur in somatic cells and are not passed to offspring.

Altering Gene Number or Position

Chromosomal changes that delete, disrupt, or rearrange many loci are usually harmful. However, when such large-scale changes leave genes intact, they may not affect the organisms' phenotype. In rare cases, chromosomal rearrangements may even be beneficial. For example, the translocation of part of one chromosome to a different chromosome could link genes in a way that produces a positive effect.

A key potential source of variation is the duplication of genes due to errors in meiosis (such as unequal crossing over), slippage during DNA replication, or the activities of transposable elements (see Concept 21.5). Duplications of large chromosome segments, like other chromosomal aberrations, are often harmful, but the duplication of smaller pieces of DNA may not be. Gene duplications that do not have severe effects can persist over generations, allowing mutations to accumulate. The result is an expanded genome with new genes that may take on new functions.

Such increases in gene number appear to have played a major role in evolution. For example, the remote ancestors of mammals had a single gene for detecting odors that has since been duplicated many times. As a result, humans today have about 380 functional olfactory receptor genes, and mice have about 1,200. This dramatic proliferation of olfactory genes probably helped early mammals, enabling them to detect faint odors and to distinguish among many different smells.

Rapid Reproduction

Mutation rates tend to be low in plants and animals, averaging about one mutation in every 100,000 genes per generation, and are often even lower in prokaryotes. But prokaryotes have many more generations per unit of time, so mutations can quickly generate genetic variation in their populations. The same is true of viruses. For instance, HIV has a generation time of about two days (that is, it takes two days for a newly formed virus to produce the next generation). HIV also has an RNA genome, which has a much higher mutation rate than a typical DNA genome due to the lack of RNA repair mechanisms in host cells (see Concept 19.2). Thus, single-drug treatments are less effective against HIV: Mutant forms of the virus, resistant to a particular drug, tend to proliferate quickly. The most effective AIDS treatments to date have been drug "cocktails" that combine several medications. This approach has worked well as it is less likely that a set of mutations that together confer resistance to *all* the drugs will occur in a short time period.

Sexual Reproduction

In organisms that reproduce sexually, most of the genetic variation in a population results from the unique combination of alleles that each individual receives from its parents. Of course, at the nucleotide level, all the differences among these alleles have originated from past mutations. Sexual reproduction then shuffles existing alleles and deals them at random to produce individual genotypes.

Three mechanisms contribute to this shuffling: crossing over, independent assortment of chromosomes, and fertilization (see Concept 13.4). During meiosis, homologous chromosomes, one inherited from each parent, trade some of their alleles by crossing over. The resulting recombinant chromosomes are then distributed at random into gametes. Then, because myriad possible mating combinations exist in a population, fertilization typically brings together gametes with different genetic backgrounds. Together, these three mechanisms ensure that sexual reproduction rearranges existing alleles into fresh combinations each generation, providing much of the genetic variation that makes evolution possible.

Mastering Biology Animation: Origins of Genetic Variation

CONCEPT CHECK 23.1

1. Explain why genetic variation within a population is a prerequisite for evolution.
2. Of all the mutations that occur in a population, why do only a small fraction become widespread?
3. **MAKE CONNECTIONS** If a population stopped reproducing sexually but still reproduced asexually, how would its genetic variation be affected over time? (See Concept 13.4.)

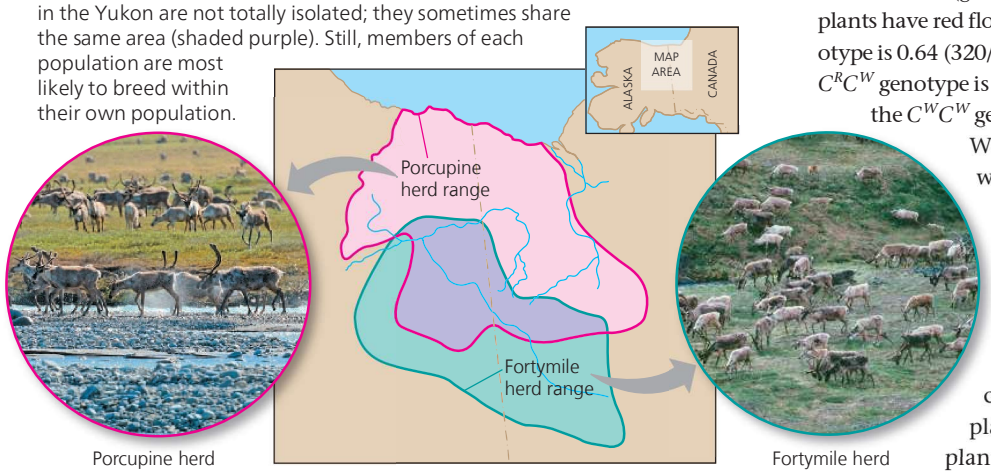
For suggested answers, see Appendix A.

CONCEPT 23.2

The Hardy-Weinberg equation can be used to test whether a population is evolving

The presence of genetic variation in a population does not guarantee that the population will evolve. For evolution to occur,

▼ Figure 23.6 One species, two populations. These two caribou populations in the Yukon are not totally isolated; they sometimes share the same area (shaded purple). Still, members of each population are most likely to breed within their own population.



one or more factors must be at work. In this section, we'll explore one way to test whether evolution is occurring in a population.

Gene Pools and Allele Frequencies

A **population** is a group of individuals of the same species that live in the same area and interbreed, producing fertile offspring. Different populations of a species may be isolated geographically from one another, exchanging genetic material only rarely. This is common for species that live on widely separated islands or in different lakes, but not all populations are isolated **(Figure 23.6)**. Still, members of a population typically breed with one another and thus are more closely related to each other than to members of other populations.

We can characterize a population's genetic makeup by describing its **gene pool**, which consists of all copies of every type of allele at every locus in all members of the population. If only one allele exists for a particular locus in a population, that allele is said to be *fixed* in the gene pool, and all individuals are homozygous for that allele. But if there are two or more alleles for a particular locus in a population, individuals may be either homozygous or heterozygous.

For example, imagine a population of 500 wildflower plants with two alleles, C^R and C^W, for a locus that codes for flower pigment. These alleles show incomplete dominance; thus, each genotype has a distinct phenotype. Plants homozygous for the C^R allele (C^RC^R) produce red pigment and have red flowers; plants homozygous for the C^W allele (C^WC^W) produce no red pigment and have white flowers; and heterozygotes (C^RC^W) produce some red pigment and have pink flowers.


C^RC^R


C^WC^W


C^RC^W

Each genotype and each allele has a frequency (proportion) in the population. To see how these frequencies are calculated, suppose our population has 320 plants with red flowers (genotype C^RC^R), 160 with pink flowers (genotype C^RC^W), and 20 with white flowers (genotype C^WC^W). Since 320 of the 500 plants have red flowers, the frequency of the C^RC^R genotype is 0.64 (320/500). Likewise, the frequency of the C^RC^W genotype is 0.32 (160/500) and the frequency of the C^WC^W genotype is 0.04 (20/500).

With respect to allele frequencies, wildflowers are diploid organisms, so each individual has two alleles for each of its genes. Hence, the 500 individuals in our population have a total of 1,000 copies of the gene for flower color. The C^R allele accounts for 800 of these copies ($320 \times 2 = 640$ for C^RC^R plants, plus $160 \times 1 = 160$ for C^RC^W plants). Thus, the frequency of the C^R allele is $800/1{,}000 = 0.8$ (80%).

When studying a locus with two alleles, the convention is to use p to represent the frequency of one allele and q to represent the frequency of the other allele. Thus, p, the frequency of the C^R allele in the gene pool of this population, is $p = 0.8$ (80%). And because there are only two alleles for this gene, the frequency of the C^W allele, represented by q, must be $q = 1 - p = 0.2$ (20%). For loci that have more than two alleles, the sum of all allele frequencies must still equal 1 (100%).

The Hardy-Weinberg Equation

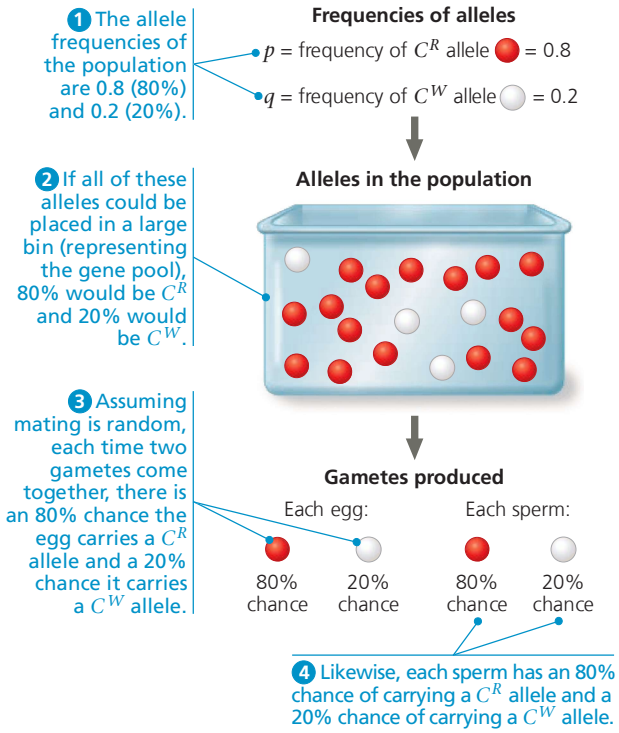
One way to assess whether natural selection or other factors are causing evolution at a particular locus is to determine what the genetic makeup of a population would be if it were *not* evolving at that locus. We can then compare that with the data we actually observed for the population. If there are no differences, this suggests that the population is not evolving. If there are differences, this suggests that the population is evolving—and then we can investigate why.

Hardy-Weinberg Equilibrium

In a population that is not evolving, allele and genotype frequencies will remain constant from generation to generation, provided that only Mendelian segregation and recombination of alleles are at work. Such a population is said to be in **Hardy-Weinberg equilibrium**, named for the British mathematician and German physician, respectively, who independently developed this idea in 1908.

To determine whether a population is in Hardy-Weinberg equilibrium, it is helpful to think about genetic crosses in a new way. Previously, we used Punnett squares to determine the genotypes of offspring in a genetic cross (see Figure 14.5). Here, instead of considering the possible allele combinations from one cross, we'll consider the combination of alleles in *all* of the crosses in a population. Imagine that all the alleles for a given locus from all the individuals in a population are placed

▼ Figure 23.7 Selecting alleles at random from a gene pool.



DRAW IT *Draw a bin with six white balls instead of four. For the frequency of C^R to remain equal to 0.8, how many red balls should the bin contain?*

Mastering Biology BioFlix® Animation: Allele Frequencies

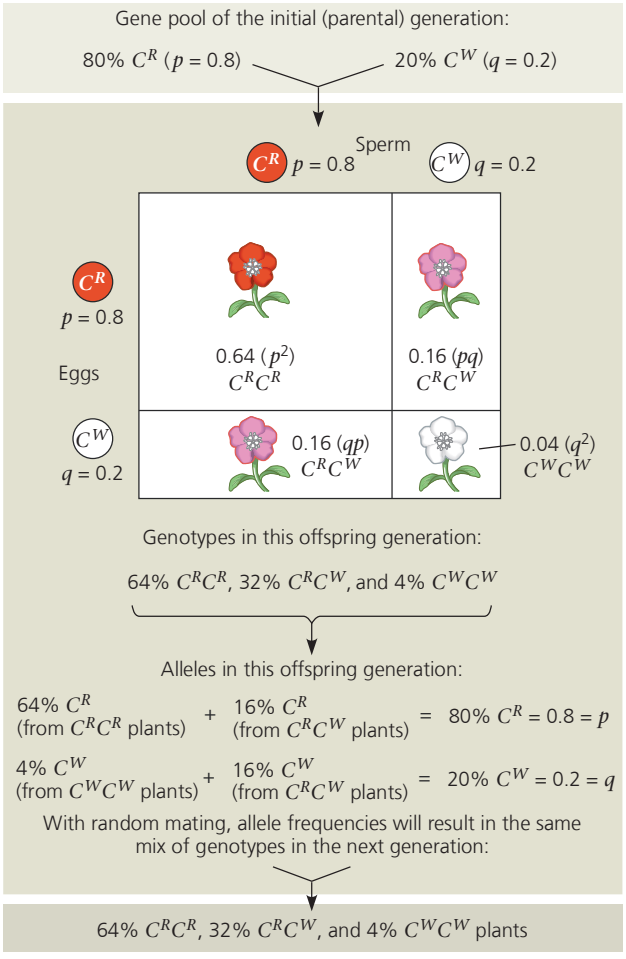
in a large bin **(Figure 23.7)**. We can think of this bin as holding the population's gene pool for that locus. "Reproduction" occurs by selecting alleles at random from the bin; somewhat similar events occur in nature when fishes release sperm and eggs into the water or when plant sperm (in pollen) is blown about by the wind. By viewing reproduction as a process of randomly selecting and combining alleles from the bin (the gene pool), we are in effect assuming that mating occurs at random: that all male-female matings are equally likely.

Let's apply the bin analogy to the hypothetical wildflower population discussed earlier. In that population of 500 flowers, the frequency of the allele for red flowers (C^R) is $p = 0.8$, and the frequency of the allele for white flowers (C^W) is $q = 0.2$. This implies that a bin holding all 1,000 copies of the flower-color gene in the population would contain 800 C^R alleles and 200 C^W alleles. Assuming that gametes are formed by selecting alleles at random from the bin, the probability that an egg or sperm contains a C^R or C^W allele is equal to the frequency of these alleles in the bin. Thus, as shown in Figure 23.7, each egg (and each sperm) has an 80% chance of containing a C^R allele and a 20% chance of containing a C^W allele.

Using the rule of multiplication (see Figure 14.9), we can now calculate the frequencies of the three possible genotypes, assuming random unions of sperm and eggs. The probability that two C^R alleles will come together is $p \times p = p^2 = 0.8 \times 0.8 = 0.64$. Thus, about 64% of the plants in the next generation will have the genotype C^RC^R. The frequency of C^WC^W individuals is expected to be about $q \times q = q^2 = 0.2 \times 0.2 = 0.04$, or 4%. C^RC^W heterozygotes can arise in two different ways. If the sperm provides the C^R allele and the egg provides the C^W allele, the resulting heterozygotes will be $p \times q = 0.8 \times 0.2 = 0.16$, or 16% of the total. If the sperm provides the C^W allele and the egg the C^R allele, the heterozygous offspring will make up $q \times p = 0.2 \times 0.8 = 0.16$, or 16%. The frequency of heterozygotes is thus the sum of these possibilities: $pq + qp = 2pq = 0.16 + 0.16 = 0.32$, or 32%.

As shown in **Figure 23.8**, the genotype frequencies in the next generation must add up to 1 (100%). Thus, the equation

▼ Figure 23.8 Hardy-Weinberg equilibrium. In our wildflower population, the gene pool remains constant from one generation to the next. Mendelian processes alone do not alter frequencies of alleles or genotypes.



WHAT IF? *If the frequency of the C^R allele were 0.6, predict the frequencies of the C^RC^R, C^RC^W, and C^WC^W genotypes.*

Mastering Biology Figure Walkthrough

for Hardy-Weinberg equilibrium states that if a population is not evolving at a locus with two alleles, the three genotypes will appear in the following proportions:

$$\underset{\substack{\text{Expected frequency of genotype } C^RC^R}}{p^2} + \underset{\substack{\text{Expected frequency of genotype } C^RC^W}}{2pq} + \underset{\substack{\text{Expected frequency of genotype } C^WC^W}}{q^2} = 1$$

Note that for a locus with two alleles, only three genotypes are possible (in this case, C^RC^R, C^RC^W, and C^WC^W). As a result, the sum of the frequencies of the three genotypes must equal 1 (100%) in *any* population regardless of whether the population is in Hardy-Weinberg equilibrium. The key point is that a population is in Hardy-Weinberg equilibrium only if the observed genotype frequency of one homozygote is p^2, the observed frequency of the other homozygote is q^2, and the observed frequency of heterozygotes is $2pq$. Finally, as suggested by Figure 23.8, if a population such as our wildflowers is in Hardy-Weinberg equilibrium and its members continue to mate randomly generation after generation, allele and genotype frequencies will remain constant. The system operates somewhat like a deck of cards: No matter how many times the deck is reshuffled to deal out new hands, the deck itself remains the same. Aces do not grow more numerous than jacks. And the repeated shuffling of a population's gene pool over the generations cannot, in itself, change the frequency of one allele relative to another.

Conditions for Hardy-Weinberg Equilibrium

The Hardy-Weinberg approach describes a population that is not evolving. This can occur if a population meets all five of the conditions for Hardy-Weinberg equilibrium listed in **Table 23.1**. But in nature, the allele and genotype frequencies of a population often *do* change over time. Such changes can occur when at least one of the conditions for Hardy-Weinberg equilibrium is not met.

Table 23.1 Conditions for Hardy-Weinberg Equilibrium

Condition	Consequence if Condition Does Not Hold
1. No mutations	The gene pool is modified if mutations occur or if entire genes are deleted or duplicated.
2. Random mating	If individuals mate within a subset of the population, such as near neighbors or close relatives (inbreeding), random mixing of gametes does not occur and genotype frequencies change.
3. No natural selection	Allele frequencies change when individuals with different genotypes show consistent differences in their survival or reproductive success.
4. Extremely large population size	In small populations, allele frequencies fluctuate by chance over time (genetic drift).
5. No gene flow	By moving alleles into or out of populations, gene flow can alter allele frequencies.

Mastering Biology Animation: Causes of Evolutionary Change

Although departure from the conditions in Table 23.1 is common—resulting in evolutionary change—it is also common for natural populations to be in Hardy-Weinberg equilibrium for specific genes. One way this can happen is if selection alters allele frequencies at some loci but not others. In addition, some populations evolve so slowly that the changes in their allele and genotype frequencies are difficult to distinguish from those predicted for a non-evolving population.

Applying the Hardy-Weinberg Equation

The Hardy-Weinberg equation is often used as an initial test of whether evolution is occurring in a population (Concept Check 23.2, question 3 is an example). The equation also has medical applications, such as estimating the percentage of a population carrying the allele for an inherited disease. For example, consider phenylketonuria (PKU), a metabolic disorder that results from homozygosity for a recessive allele. This disorder occurs in about one out of every 10,000 babies born in the United States. Left untreated, PKU results in mental disability and other problems. (As described in Concept 14.4, newborns are now routinely tested for PKU, and symptoms can be largely avoided with a diet very low in phenylalanine.)

To apply the Hardy-Weinberg equation, we must assume that no new PKU mutations are being introduced into the population (condition 1) and that people neither choose their mates on the basis of whether or not they carry this gene nor generally mate with close relatives (condition 2). We must also ignore any effects of differential survival and reproductive success among PKU genotypes (condition 3) and assume that there are no effects of genetic drift (condition 4) or of gene flow from other populations into the United States (condition 5). These assumptions are reasonable: The mutation rate for the PKU gene is low, inbreeding and other forms of nonrandom mating are not common in the United States, selection occurs only against the rare homozygotes (and then only if dietary restrictions are not followed), the U.S. population is very large, and populations outside the country have PKU allele frequencies similar to those seen in the United States.

If all these assumptions hold, then the frequency of individuals in the population born with PKU will correspond to q^2 in the Hardy-Weinberg equation (q^2 = frequency of homozygotes). Because the allele is recessive, we must estimate the number of heterozygotes rather than counting them directly as we did with the pink flowers. Recall that there is one PKU occurrence per 10,000 births, which indicates that $q^2 = 0.0001$. Thus, the frequency (q) of the recessive allele for PKU is

$$q = \sqrt{0.0001} = 0.01$$

and the frequency of the dominant allele is

$$p = 1 - q = 1 - 0.01 = 0.99$$

Scientific Skills Exercise

Using the Hardy-Weinberg Equation to Interpret Data and Make Predictions

Is Evolution Occurring in a Soybean Population? One way to test whether evolution is occurring in a population is to compare the observed genotype frequencies at a locus with those expected for a non-evolving population based on the Hardy-Weinberg equation. In this exercise, you will test whether a soybean population is evolving at a locus with two alleles, C^G and C^Y, that affect chlorophyll production and hence leaf color.

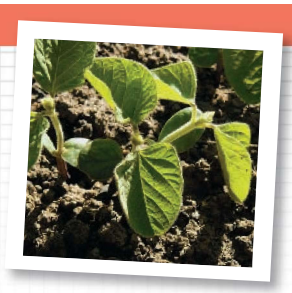
How the Experiment Was Done Students planted soybean seeds and then counted the number of seedlings of each genotype at day 7 and again at day 21. Seedlings of each genotype could be distinguished visually because the C^G and C^Y alleles show incomplete dominance: C^GC^G seedlings have green leaves, C^GC^Y seedlings have green-yellow leaves, and C^YC^Y seedlings have yellow leaves.

Data from the Experiment

Time (days)	Number of Seedlings			
	Green (C^GC^G)	Green-yellow (C^GC^Y)	Yellow (C^YC^Y)	Total
7	49	111	56	216
21	47	106	20	173

INTERPRET THE DATA

1. Use the observed genotype frequencies from the day 7 data to calculate the frequencies of the C^G allele (p) and the C^Y allele (q).
2. Next, use the Hardy-Weinberg equation ($p^2 + 2pq + q^2 = 1$) to calculate the day 7 expected frequencies of genotypes C^GC^G, C^GC^Y, and C^YC^Y for a population in Hardy-Weinberg equilibrium.
3. (a) Calculate the observed frequencies of genotypes C^GC^G, C^GC^Y, and C^YC^Y at day 7. **(b)** Compare these frequencies to the expected frequencies calculated in question 2. Is the seedling population in Hardy-Weinberg equilibrium at day 7, or is evolution occurring? Explain your reasoning and identify which genotypes, if any, appear to be selected for or against.
4. (a) Calculate the observed frequencies of genotypes C^GC^G, C^GC^Y, and C^YC^Y at day 21. **(b)** Compare these frequencies to the expected frequencies calculated in question 2 and to the observed frequencies at day 7. Is the seedling population in Hardy-Weinberg equilibrium at day 21, or is evolution occurring? Explain your reasoning and identify which genotypes, if any, appear to be selected for or against.
5. Homozygous C^YC^Y individuals cannot produce chlorophyll. The ability to photosynthesize becomes more critical as seedlings age and begin to exhaust the supply of food that was stored in the seed from which they emerged. Develop a hypothesis that explains the data for days 7 and 21. Based on this hypothesis, predict how the frequencies of the C^G and C^Y alleles will change beyond day 21.



Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

The frequency of carriers, heterozygous people who do not have PKU but may pass the PKU allele to offspring, is

$$2pq = 2 \times 0.99 \times 0.01 = 0.0198$$
(approximately 2% of the U.S. population)

Remember, the assumption of Hardy-Weinberg equilibrium yields an approximation; the real number of carriers may differ. Still, our calculations suggest that harmful recessive alleles at this and other loci can be concealed in a population because they are carried by healthy heterozygotes. The **Scientific Skills Exercise** provides another opportunity for you to apply the Hardy-Weinberg equation to allele data.

CONCEPT CHECK 23.2

1. A population has 85 individuals of genotype *AA*, 320 of genotype *Aa*, and 295 of genotype *aa*. Calculate the genotype frequencies and the frequencies of alleles *A* and *a*.
2. The frequency of allele *a* is 0.45 for a population in Hardy-Weinberg equilibrium. What are the expected frequencies of genotypes *AA*, *Aa*, and *aa*?
3. **WHAT IF?** A locus that affects susceptibility to a degenerative brain disease has two alleles, *V* and *v*. In a population, 16 people have genotype *VV*, 92 have genotype *Vv*, and 12 have genotype *vv*. Is this population evolving? Explain.

For suggested answers, see Appendix A.

CONCEPT 23.3

Natural selection, genetic drift, and gene flow can alter allele frequencies in a population

Note again the five conditions required for a population to be in Hardy-Weinberg equilibrium (see Table 23.1). A deviation from any of these conditions is a potential cause of evolution. New mutations (violation of condition 1) can alter allele frequencies, but because mutations are rare, the change from one generation to the next is likely to be very small. Nonrandom mating (violation of condition 2) can affect the frequencies of homozygous and heterozygous genotypes but by itself has no effect on allele frequencies in the gene pool. (Allele frequencies can change if individuals with certain inherited traits are more likely than other individuals to obtain mates. However, such a situation not only causes a deviation from random mating, but also violates condition 3, no natural selection.)

For the rest of this section we will focus on the three mechanisms that alter allele frequencies directly and cause most evolutionary change: natural selection, genetic drift, and gene flow (violations of conditions 3–5).

Natural Selection

The concept of natural selection is based on differential success in survival and reproduction: Individuals in a population exhibit variations in their heritable traits, and those with traits that are better suited to their environment tend to produce more offspring than those with traits that are not as well suited.

In genetic terms, selection results in alleles being passed to the next generation in proportions that differ from the present generation. For example, the fruit fly *D. melanogaster* has an allele that confers resistance to the insecticide DDT. This allele has a frequency of 0% in laboratory strains of *D. melanogaster* from flies collected in the wild in the early 1930s, prior to DDT use. However, in strains established from flies collected after 1960 (following 20 or more years of DDT use), the allele frequency is 37%. Thus, this allele either arose by mutation between 1930 and 1960 or was present in 1930, but very rare. In any case, the rise in frequency of this allele most likely occurred because DDT is an effective poison that is a strong selective force in exposed fly populations.

As the *D. melanogaster* example suggests, an allele that confers resistance to an insecticide will increase in frequency in a population exposed to that insecticide. Such changes are not coincidental. By consistently favoring some alleles over others, natural selection can cause **adaptive evolution**, in which traits that enhance survival or reproduction tend to increase in frequency over time. We'll explore this process in Concept 23.4.

Genetic Drift

If you flip a coin 1,000 times, a result of 700 heads and 300 tails might make you suspicious about that coin. But if you flip a coin only 10 times, an outcome of 7 heads and 3 tails would not be surprising. The smaller the number of coin flips, the more likely it is that chance alone will cause a deviation from the predicted result. (In this case, the prediction is an equal number of heads and tails.) Chance events can also cause allele frequencies to fluctuate unpredictably from one generation to the next, especially in small populations—a process called **genetic drift**.

Figure 23.9 models how genetic drift might affect a small population of our wildflowers. In this example, drift leads to the loss of an allele from the gene pool, but it is a matter of chance that the C^W allele is lost and not the C^R allele. Such unpredictable changes in allele frequencies can be caused by chance events associated with survival and reproduction. Perhaps a large animal such as a moose stepped on the three C^WC^W individuals in generation 2, killing them and increasing the chance that only the C^R allele would be passed to the next generation. Allele frequencies can also be affected by chance events that occur during fertilization. For example, suppose two individuals of genotype C^RC^W had a small number of offspring. By chance alone, every egg and sperm pair that generated offspring could happen to have carried the C^R allele and not the C^W allele.

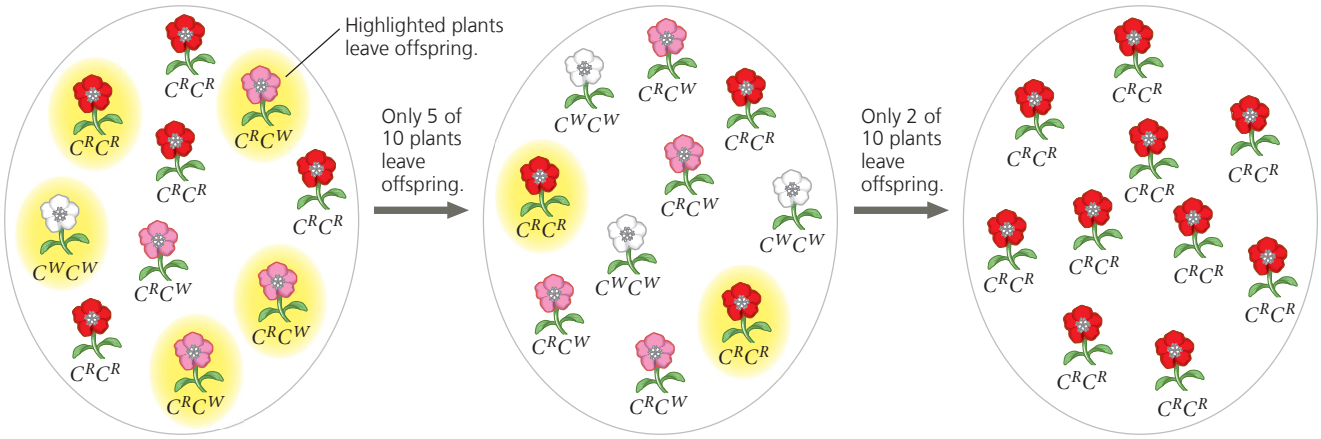
Certain circumstances can result in genetic drift having a significant impact on a population. Two examples are the founder effect and the bottleneck effect.

The Founder Effect

When a few individuals become isolated from a larger population, this smaller group may establish a new population whose gene pool differs from the source population; this is called the **founder effect**. The founder effect might occur, for example, when a few members of a population are blown by a storm to a new island. Genetic drift, in which chance events alter allele frequencies, can occur in such a case because the

▼ Figure 23.9 Genetic drift. This small wildflower population has a stable size of ten plants. Suppose that by chance only five plants of generation 1 (those highlighted in yellow) produce fertile offspring. Again by chance, only two plants of generation 2 leave fertile offspring.

VISUAL SKILLS *Based on this diagram, summarize how the frequency of the* C^W *allele changes over time.*



storm indiscriminately transports some individuals (and their alleles), but not others, from the source population.

The founder effect probably accounts for the relatively high frequency of certain inherited disorders among isolated human populations. For example, in 1814, 15 British colonists founded a settlement on Tristan da Cunha, a group of small islands in the Atlantic Ocean midway between Africa and South America. Apparently, one of the colonists carried a recessive allele for retinitis pigmentosa, a progressive form of blindness that affects homozygous individuals. Of the founding colonists' 240 descendants on the island in the late 1960s, four had retinitis pigmentosa. The frequency of the allele that causes this disease is ten times higher on Tristan da Cunha than in the populations from which the founders came.

The Bottleneck Effect

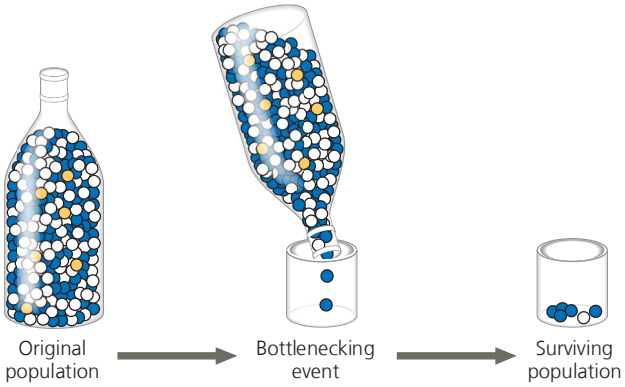
A sudden change in the environment, such as a fire or flood, may drastically reduce the size of a population. A severe drop in population size can cause the **bottleneck effect**, so named because the population has passed through a "bottleneck" that greatly reduces its size **(Figure 23.10)**. By chance alone, certain alleles may be overrepresented among the survivors, others may be underrepresented, and some may be absent altogether. Ongoing genetic drift is likely to have substantial effects on the gene pool until the population becomes large enough that chance events have less impact. But even if a population that has passed through a bottleneck ultimately recovers in size, it may have low levels of genetic variation for a long period of time—a legacy of the genetic drift that occurred when the population was small.

Case Study: *Impact of Genetic Drift on the Greater Prairie Chicken*

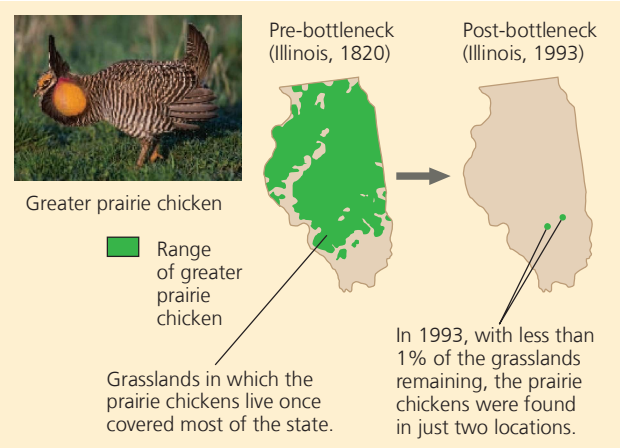
Human actions sometimes create severe bottlenecks. Millions of greater prairie chickens (*Tympanuchus cupido*) once lived on the prairies of Illinois. As these prairies were converted to farmland during the 1800s and 1900s, the number of greater prairie chickens plummeted **(Figure 23.11a)**. By 1993 fewer than 50 birds remained. These few surviving birds had low levels of genetic variation, and less than 50% of their eggs hatched, compared with much higher hatching rates of the larger populations in Kansas and Nebraska **(Figure 23.11b)**.

These data suggest that genetic drift during the bottleneck may have led to a loss of genetic variation and an increase in the frequency of harmful alleles. To investigate this hypothesis, researchers extracted DNA from 15 museum specimens of Illinois greater prairie chickens. Of the 15 birds, 10 had been collected in the 1930s, when there were 25,000 greater prairie chickens in Illinois, and 5 had been collected in the 1960s, when there were 1,000 greater prairie chickens in Illinois. By studying the DNA of these specimens, the researchers were able to obtain a minimum, baseline estimate of how much genetic variation was present in the Illinois population *before* the population shrank to extremely low numbers. This baseline estimate is a key piece of information that is not usually available in cases of population bottlenecks.

▼ Figure 23.10 The bottleneck effect. Shaking a few marbles through the neck of a bottle is analogous to a drastic reduction in the size of a population. By chance, blue marbles are overrepresented in the surviving population and gold marbles are absent.



▼ Figure 23.11 Genetic drift and loss of genetic variation.



(a) The Illinois population of greater prairie chickens dropped from millions of birds in the 1800s to fewer than 50 birds in 1993.

Location	Population size	Number of alleles per locus	Percentage of eggs hatched
Illinois			
1930–1960s	1,000–25,000	5.2	93
1993	<50	3.7	<50
Kansas, 1998 (no bottleneck)	750,000	5.8	99
Nebraska, 1998 (no bottleneck)	75,000–200,000	5.8	96

(b) In the small Illinois population, genetic drift led to decreases in the number of alleles per locus and the percentage of eggs hatched.

The researchers surveyed six loci and found that the 1993 population had fewer alleles per locus than the pre-bottleneck Illinois or the current Kansas and Nebraska populations (see Figure 23.11b). Thus, as predicted, drift had reduced the genetic variation of the small 1993 population. Drift may also have increased the frequency of harmful alleles, leading to the low egg-hatching rate. To counteract these negative effects, 271 birds from neighboring states were added to the Illinois population over four years. This strategy succeeded: New alleles entered the population, and the egg-hatching rate improved to over 90%. Overall, studies on the Illinois greater prairie chicken illustrate the powerful effects of genetic drift in small populations and provide hope that in at least some populations, these effects can be reversed.

Effects of Genetic Drift: A Summary

The examples we've described highlight four key points:

1. **Genetic drift is significant in small populations.** Chance events can cause an allele to be disproportionately over- or underrepresented in the next generation. Although chance events occur in populations of all sizes, they tend to alter allele frequencies substantially only in small populations.
2. **Genetic drift can cause allele frequencies to change at random.** Because of genetic drift, an allele may increase in frequency one year, then decrease the next; the change from year to year is not predictable. Thus, unlike natural selection, which in a given environment consistently favors some alleles over others, genetic drift causes allele frequencies to change at random over time.
3. **Genetic drift can lead to a loss of genetic variation within populations.** By causing allele frequencies to fluctuate randomly over time, genetic drift can eliminate alleles from a population. Because evolution depends on genetic variation, such losses can influence how effectively a population can adapt to a change in the environment.
4. **Genetic drift can cause harmful alleles to become fixed.** Alleles that are neither harmful nor beneficial can be lost or become fixed (reach a frequency of 100%) by chance through genetic drift. In very small populations, genetic drift can also cause alleles that are slightly harmful to become fixed. When this occurs, the population's survival can be threatened (as in greater prairie chickens).

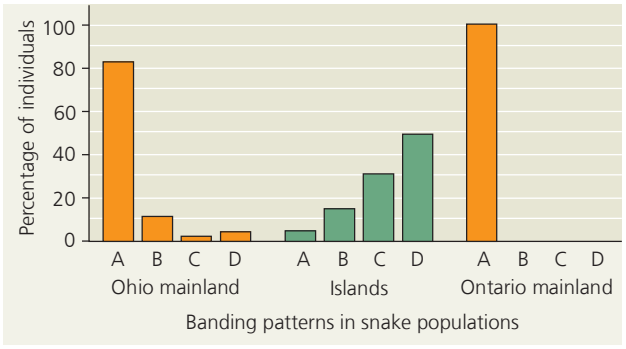
Gene Flow

Natural selection and genetic drift are not the only phenomena affecting allele frequencies. Allele frequencies can also change by **gene flow**, the transfer of alleles into or out of a population due to the movement of fertile individuals or their gametes. For example, suppose that near our original hypothetical wildflower population there is another population consisting primarily of white-flowered individuals (C^WC^W). Insects carrying pollen from these plants may fly to and pollinate plants in our original population. The introduced C^W alleles would modify our original population's allele frequencies in the next generation. Because alleles are transferred between populations, gene flow tends to reduce the genetic differences between populations. In fact, if it is extensive enough, gene flow can result in two populations combining into a single population with a common gene pool.

Alleles transferred by gene flow can also affect how well populations are adapted to local environmental conditions. For instance, mainland and island populations of the Lake Erie water snake (*Nerodia sipedon*) differ in their color patterns **(Figure 23.12)**: Nearly all snakes from the Ohio or Ontario mainlands are strongly banded, whereas the majority of snakes

▼ Figure 23.12 Gene flow and local adaptation in the Lake Erie water snake (*Nerodia sipedon*). Researchers assigned letters to variations in coloration in *N. sipedon* populations. Color pattern A is strong banding, patterns B and C are intermediate banding, and pattern D is no banding. Banding is advantageous for camouflage in mainland environments, whereas having no bands is advantageous in island environments. However, gene flow from the mainland causes banding to persist in island populations.





WHAT IF? *Suppose a severe weather event caused island populations to decrease in size but did not affect the size of mainland populations. Predict how gene flow from the mainland would affect color patterns in island populations in the year immediately after the storm. Explain.*

from islands are unbanded or intermediate. Banding coloration is an inherited trait, determined by a few loci (with alleles that encode bands being dominant to alleles that encode the absence of bands). On islands, water snakes live along rocky shorelines, while on the mainland, they live in marshes. Snakes without bands are more well camouflaged in island habitats than are snakes with bands. Hence, on islands, snakes without bands survive at higher rates than do snakes with bands.

These data indicate that snakes without bands are favored by natural selection in island populations. Thus, we might expect that *all* snakes on islands would lack bands. Why is this not the case? The answer lies in gene flow from the mainland. In any given year, three to ten snakes from the mainland swim to the islands and join the populations there. As a result, each year such migrants transfer alleles for banded coloration from the mainland (where nearly all snakes have bands) to the islands. This ongoing gene flow has prevented selection from removing all of the alleles for banded coloration from island populations—thereby preventing island populations from adapting fully to local conditions.

Gene flow can also transfer alleles that improve the ability of populations to adapt to local conditions. For example, gene flow has resulted in the worldwide spread of several insecticide resistance alleles in the mosquito *Culex pipiens*, a vector of West Nile virus and other diseases. Each of these alleles has a unique genetic signature that allowed researchers to document that it arose by mutation in only one or a few geographic locations. In their population of origin, these alleles increased because they provided insecticide resistance. These alleles were then transferred by gene flow to other populations exposed to insecticides, where again, their frequencies increased as a result of natural selection.

Finally, gene flow has become an increasingly important agent of evolutionary change in human populations. Humans today move much more freely about the world than in the past. As a result, mating is more common between members of populations that previously had very little contact, leading to an exchange of alleles and fewer genetic differences between those populations.

Mastering Biology **BioFlix® Animation: Natural Selection, Genetic Drift, and Gene Flow**

CONCEPT CHECK 23.3

1. In what sense is natural selection more "predictable" than genetic drift?
2. Distinguish genetic drift from gene flow in terms of (a) how they occur and (b) their implications for future genetic variation in a population.
3. **WHAT IF?** Suppose two plant populations exchange pollen and seeds. In one population, individuals of genotype *AA* are most common (9,000 *AA*, 900 *Aa*, 100 *aa*), while the opposite is true in the other population (100 *AA*, 900 *Aa*, 9,000 *aa*). If neither allele has a selective advantage, what will happen over time to the allele and genotype frequencies of these populations?

For suggested answers, see Appendix A.

CONCEPT 23.4

Natural selection is the only mechanism that consistently causes adaptive evolution

Evolution by natural selection is a blend of chance and "sorting": chance in the creation of new genetic variations (as in mutation) and sorting as natural selection favors some alleles over others. Because of this favoring process, the outcome of natural selection is *not* random. Instead, natural selection consistently increases the frequencies of alleles that provide reproductive advantage, thus leading to adaptive evolution.

Natural Selection: *A Closer Look*

To see how natural selection can cause adaptive evolution, we'll begin with the concept of relative fitness and the different ways that selection acts on an organism's phenotype.

Relative Fitness

The phrases "struggle for existence" and "survival of the fittest" are commonly used to describe natural selection, but these expressions are misleading if always taken to mean direct competitive contests among individuals. There *are* animal species in which individuals, usually the males, lock horns or otherwise do combat to determine mating privilege. But reproductive success is generally more subtle and depends on many factors besides outright battle. For example, a barnacle that is more efficient at collecting food than its neighbors may have greater stores of energy and hence be able to produce a larger number of eggs. A moth may have more offspring than other moths in the same population because its body colors more effectively conceal it from predators, improving its chance of surviving long enough to produce more offspring. These examples illustrate how in a given environment, certain traits can lead to greater **relative fitness**: the contribution an individual makes to the gene pool of the next generation *relative to* the contributions of other individuals.

Although we often refer to the relative fitness of a genotype, remember that the entity that is subjected to natural selection is the whole organism, not the underlying genotype. Thus, selection acts more directly on the phenotype than on the genotype; it acts on the genotype indirectly, via how the genotype affects the phenotype.

Directional, Disruptive, and Stabilizing Selection

Natural selection can alter the frequency distribution of heritable traits in three ways, depending on which phenotypes in a population are favored: through directional selection, disruptive selection, and stabilizing selection.

Directional selection occurs when conditions favor individuals exhibiting one extreme of a phenotypic

range, thereby shifting a population's frequency curve for the phenotypic character in one direction or the other **(Figure 23.13a)**. Directional selection is common when a population's environment changes or when members of a population migrate to a new (and different) habitat. For instance, an increase in the relative abundance of large seeds over small seeds led to an increase in beak depth in a population of Galápagos finches (see Figure 23.2).

Disruptive selection **(Figure 23.13b)** occurs when conditions favor individuals at both extremes of a phenotypic range over individuals with intermediate phenotypes. One example is a population of black-bellied seedcracker finches in Cameroon whose members display two distinctly different beak sizes. Small-billed birds feed mainly on soft seeds, whereas large-billed birds specialize in cracking hard seeds. It appears that birds with intermediate-sized bills are relatively inefficient at cracking both types of seeds and thus have lower relative fitness.

Stabilizing selection **(Figure 23.13c)** acts against both extreme phenotypes and favors intermediate variants. This mode of selection reduces variation and tends to maintain the status quo for a particular phenotypic character. For example, the birth weights of most human babies lie in the range of 3–4 kg (6.6–8.8 pounds). Babies who are much smaller suffer considerably higher rates of mortality; babies who are much larger show a slight increase in mortality.

Regardless of which type of selection occurs, however, the basic mechanism remains the same. Selection favors individuals whose heritable phenotypic traits provide higher reproductive success than do the traits of other individuals.

Mastering Biology **HHMI Video: Selection for Tuskless Elephants**

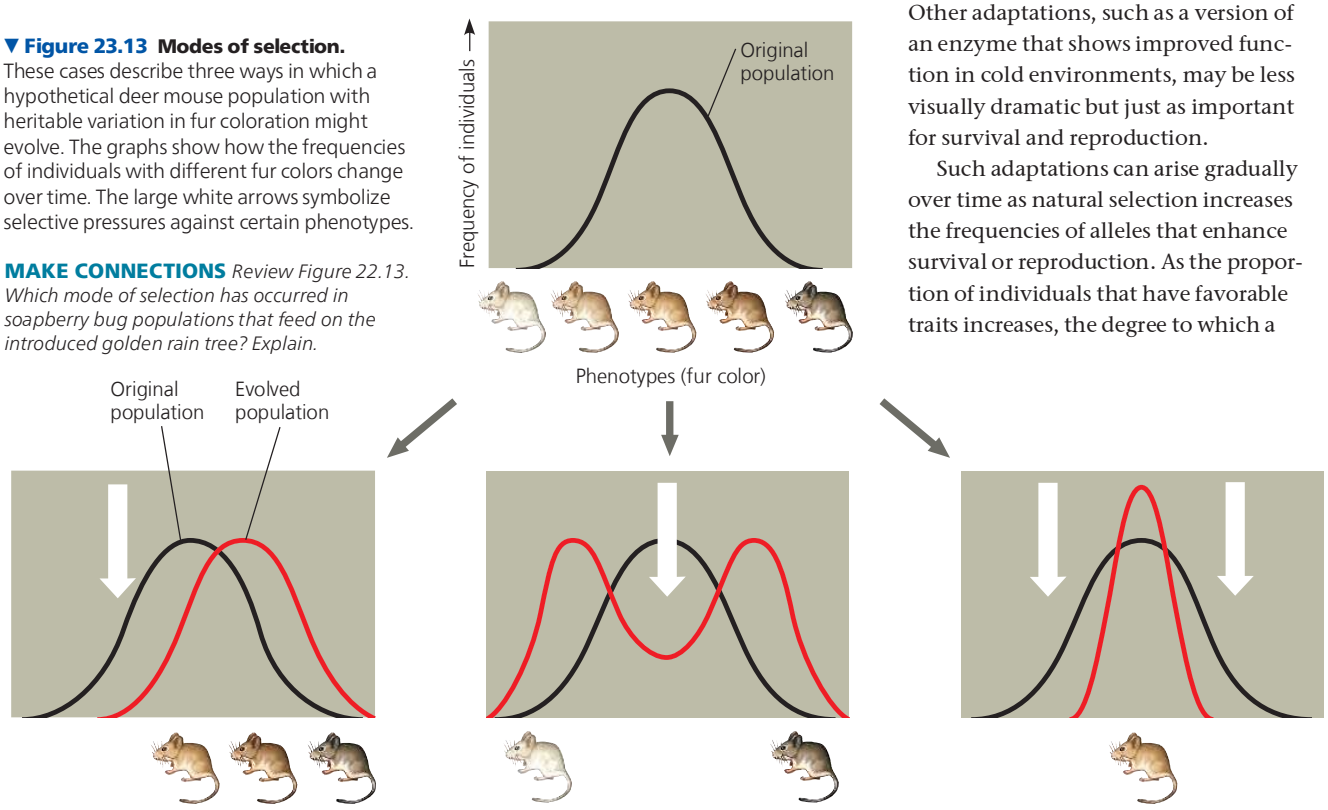
The Key Role of Natural Selection in Adaptive Evolution

The adaptations of organisms include many striking examples. Certain octopuses, for example, have the ability to change color rapidly, enabling them to blend into different backgrounds. Another example is the remarkable jaws of snakes **(Figure 23.14)**, which allow them to swallow prey much larger than their own head (a feat analogous to a person swallowing a whole watermelon). Other adaptations, such as a version of an enzyme that shows improved function in cold environments, may be less visually dramatic but just as important for survival and reproduction.

Such adaptations can arise gradually over time as natural selection increases the frequencies of alleles that enhance survival or reproduction. As the proportion of individuals that have favorable traits increases, the degree to which a

▼ Figure 23.13 Modes of selection.
These cases describe three ways in which a hypothetical deer mouse population with heritable variation in fur coloration might evolve. The graphs show how the frequencies of individuals with different fur colors change over time. The large white arrows symbolize selective pressures against certain phenotypes.

MAKE CONNECTIONS *Review Figure 22.13. Which mode of selection has occurred in soapberry bug populations that feed on the introduced golden rain tree? Explain.*

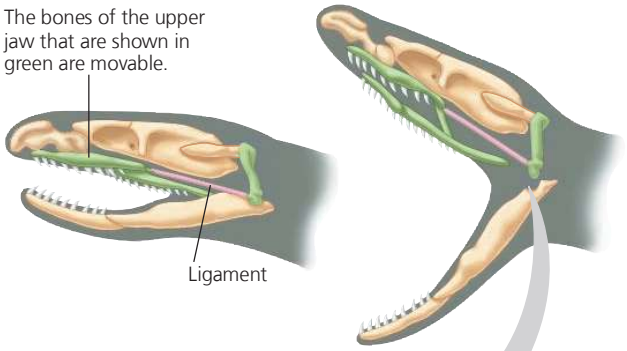


(a) Directional selection shifts the overall makeup of the population by favoring variants that are at one extreme of the distribution. In this case, lighter mice are selected against because they live among dark rocks, making it harder for them to hide from predators.

(b) Disruptive selection favors variants at both ends of the distribution. These mice have colonized a patchy habitat made up of light and dark rocks, with the result that mice of an intermediate color are selected against.

(c) Stabilizing selection removes extreme variants from the population and preserves intermediate types. If the environment consists of rocks of an intermediate color, both light and dark mice will be selected against.

▼ Figure 23.14 Movable jaw bones in snakes.



The skull bones of most terrestrial vertebrates are relatively rigidly attached to one another, limiting jaw movement. In contrast, most snakes have movable bones in their upper jaw, allowing them to swallow food much larger than their head.



species is well suited for life in its environment improves; that is, adaptive evolution occurs. However, the physical and biological components of an organism's environment may change over time. As a result, what constitutes a "good match" between an organism and its environment can be a moving target, making adaptive evolution a continuous, dynamic process. Environmental conditions can also differ from place to place, causing different alleles to be favored in different locations. When this occurs, natural selection can cause the populations of a species to differ genetically from one another.

And what about genetic drift and gene flow? Both can, in fact, increase the frequencies of alleles that enhance survival or reproduction, but neither does so consistently. Genetic drift can cause the frequency of a slightly beneficial allele to increase, or, alternately, to decrease. Similarly, gene flow may introduce alleles that are advantageous or ones that are disadvantageous. Natural selection is the only evolutionary mechanism that consistently leads to adaptive evolution.

Mastering Biology HHMI Video: Got Lactase?
The Co-Evolution of Genes and Culture

Sexual Selection

Charles Darwin was the first to explore the implications of **sexual selection**, a process in which individuals with certain inherited characteristics are more likely than other individuals of the same sex to obtain mates. Sexual selection can result in **sexual dimorphism**, a difference in secondary



▲ Figure 23.15 Sexual dimorphism and sexual selection. A peacock (left) and a peahen (right) show extreme sexual dimorphism. There is intrasexual selection between competing males, followed by intersexual selection when the females choose among the showiest males.

sexual characteristics between males and females of the same species **(Figure 23.15)**. These distinctions include differences in size, color, ornamentation, and behavior.

How does sexual selection operate? There are several ways. In **intrasexual selection**, meaning selection within the same sex, individuals of one sex compete directly for mates of the opposite sex. In many species, intrasexual selection occurs among males. For example, a single male may patrol a group of females and prevent other males from mating with them. The patrolling male may defend his status by defeating smaller, weaker, or less fierce males in combat. More often, this male is the psychological victor in ritualized displays that discourage would-be competitors but do not risk injury that would reduce his own fitness (see Figure 51.16). Intrasexual selection also occurs among females in a variety of species, including ring-tailed lemurs and broadnosed pipefish.

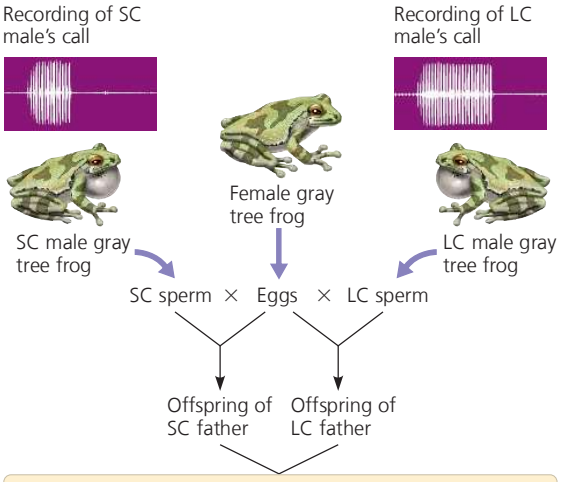
In **intersexual selection**, also called *mate choice*, individuals of one sex (usually the females) are choosy in selecting their mates from the other sex. In many cases, the female's choice depends on the showiness of the male's appearance or behavior (see Figure 23.15). What intrigued Darwin about mate choice is that male showiness may not seem adaptive in any other way and may in fact pose some risk. For example, bright plumage may make male birds more visible to predators. But if such characteristics help a male gain a mate, and if this benefit outweighs the risk from predation, then both the bright plumage and the female preference for it will be reinforced because they enhance overall reproductive success.

How do female preferences for certain male characteristics evolve in the first place? One hypothesis is that females prefer male traits that are correlated with "good genes." If the trait preferred by females is indicative of a male's overall genetic quality, both the male trait and female preference

▼ Figure 23.16 Inquiry

Do females select mates based on traits indicative of "good genes"?

Experiment Female gray tree frogs (*Hyla versicolor*) prefer to mate with males that give long mating calls. To test whether the genetic makeup of long-calling (LC) males is superior to that of short-calling (SC) males, researchers fertilized half the eggs of each female with sperm from an LC male and the other half with sperm from an SC male. In two separate experiments (one in 1995, one in 1996), the resulting half-sibling offspring were raised in a common environment, and their survival and growth were monitored.



Results

Offspring Performance	1995	1996
Larval survival	LC better	NSD
Larval growth	NSD	LC better
Time to metamorphosis	LC better (shorter)	LC better (shorter)

NSD = no significant difference; LC better = offspring of LC males superior to offspring of SC males.

Conclusion Because offspring fathered by an LC male outperformed their half-siblings fathered by an SC male, the team concluded that the duration of a male's mating call is indicative of the male's overall genetic quality. This result supports the hypothesis that female mate choice can be based on a trait that indicates whether the male has "good genes."

Data from A. M. Welch et al., Call duration as an indicator of genetic quality in male gray tree frogs, *Science* 280:1928–1930 (1998).

INQUIRY IN ACTION Read and analyze the original paper in *Inquiry in Action: Interpreting Scientific Papers.*

WHAT IF? *Why did the researchers split each female frog's eggs into two batches for fertilization by different males? Why didn't they mate each female with a single male frog?*

for it should increase in frequency. **Figure 23.16** describes one experiment testing this hypothesis in gray tree frogs.

In several bird species, the traits preferred by females are related to overall male health. Here, too, female preference appears to be based on traits that reflect "good genes"—in this case, alleles indicative of a robust immune system.

Balancing Selection

As we've seen, genetic variation is often found at loci affected by selection. What prevents natural selection from reducing the variation at those loci by culling all unfavorable alleles? As mentioned earlier, in diploid organisms, many unfavorable recessive alleles persist because they are hidden from selection when in heterozygous individuals. In addition, selection itself may preserve variation at some loci, thus maintaining two or more phenotypic forms in a population. Known as **balancing selection**, this type of selection includes frequency-dependent selection and heterozygote advantage.

Frequency-Dependent Selection

In **frequency-dependent selection**, the fitness of a phenotype depends on how common it is in the population. Consider the scale-eating fish (*Perissodus microlepis*) of Lake Tanganyika, in Africa. These fish attack other fish from behind, darting in to remove a few scales from the flank of their prey. Of interest here is a peculiar feature of the scale-eating fish: Some are "left-mouthed" and some are "right-mouthed."

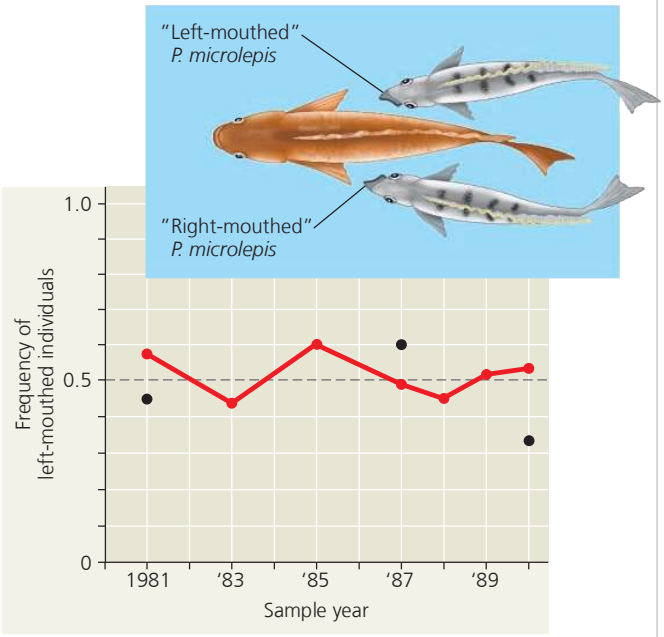
Because their mouth twists to the left, left-mouthed fish typically attack their prey's right flank **(Figure 23.17)**. (To see why, twist your lower jaw and lips to the left and imagine trying to take a bite from the left side of a fish, approaching it from behind.) Similarly, right-mouthed fish attack from the left. Prey species guard against attack from whatever phenotype of scale-eating fish is most common. Thus, from year to year, selection favors whichever mouth phenotype is least common. As a result, the frequency of left- and right-mouthed fish oscillates over time, and this balancing selection keeps the frequency of each phenotype close to 50%.

Heterozygote Advantage

If individuals who are heterozygous at a particular locus have greater fitness than do both kinds of homozygotes, they exhibit **heterozygote advantage**. In such a case, natural selection tends to maintain two or more alleles at that locus. Note that heterozygote advantage is defined in terms of *genotype*, not phenotype. Thus, whether heterozygote advantage represents stabilizing or directional selection depends on the relationship between the genotype and the phenotype. For example, if the phenotype of a heterozygote is intermediate to the phenotypes of both homozygotes, then heterozygote advantage is a form of stabilizing selection.

An example of heterozygote advantage occurs at the locus in humans that codes for the β polypeptide subunit of hemoglobin, the oxygen-carrying protein of red blood cells. In homozygous individuals, a recessive allele at that locus causes sickle-cell disease. The red blood cells of people with sickle-cell disease become distorted in shape, or *sickled*, under low-oxygen conditions (see Figure 5.19). These sickled cells can clump together and block the flow of blood in the capillaries, damaging organs such as the kidney, heart, and brain. Although some red blood cells become sickled in

▼ Figure 23.17 Frequency-dependent selection. In a population of the scale-eating fish *Perissodus microlepis*, the frequency of left-mouthed individuals (red data points) rises and falls in a regular manner. The black data points indicate the frequency of left-mouthed individuals among adults that reproduced in three sample years.



INTERPRET THE DATA *For 1981, 1987, and 1990, compare the frequency of left-mouthed individuals among breeding adults to the frequency of left-mouthed individuals in the entire population. What do the data indicate about when natural selection favors left-mouthed individuals over right-mouthed individuals (or vice versa)? Explain.*

heterozygotes, not enough become sickled to cause sickle-cell disease.

As described in **Figure 23.18**, heterozygotes for the sickle-cell allele are protected against the most severe effects of malaria, a disease caused by a parasite that infects red blood cells. One reason for this partial protection is that the body destroys sickled red blood cells rapidly, killing the parasites they harbor. Malaria is a major killer in some tropical regions. In such regions, selection favors heterozygotes over homozygous dominant individuals, who are more vulnerable to the effects of malaria, and also over homozygous recessive individuals, who develop sickle-cell disease. These selective pressures have caused the frequency of the sickle-cell allele to reach relatively high levels in areas where the malaria parasite, which is carried by mosquitoes, is common.

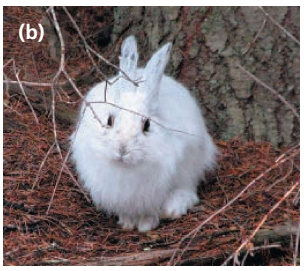
Why Natural Selection Cannot Fashion Perfect Organisms

Though natural selection leads to adaptation, nature abounds with examples of organisms that are less than ideally suited for their lifestyles. There are several reasons why.

1. **Selection can act only on existing variations.** Natural selection favors only the fittest phenotypes among those currently in the population, which may not be the ideal traits. New advantageous alleles do not arise on demand. For example, historically, snowshoe hares (*Lepus americanus*) have molted, changing their coats from brown to white, at a time of year that matched the onset of snowfall, providing camouflage all winter. But due to climate change, the first snowfall now occurs later in the year. In some populations, the date at which the hares change their coat color has remained the same, causing the hares to be poorly camouflaged early in winter and thus easier for predators to spot and kill **(Figure 23.19)**. Because their gene pools lack alleles that could delay when molting occurs, these populations have been unable to adapt to changing conditions.
2. **Evolution is limited by historical constraints.** Each species has a legacy of descent with modification from ancestral forms. Evolution does not scrap the ancestral anatomy and build each new complex structure from scratch; rather, evolution co-opts existing structures and adapts them to new situations. We could imagine that if a terrestrial animal were to adapt to an environment in which flight would be advantageous, it might be best just to grow an extra pair of limbs that would serve as wings. However, evolution does not work this way; instead, it operates on the traits an organism already has. Thus, in birds and bats, an existing pair of limbs took on new functions for flight as these organisms evolved from nonflying ancestors.
3. **Adaptations are often compromises.** Each organism must do many different things. A seal spends part of its time on rocks; it could probably walk better if it had legs instead of flippers, but then it would not swim nearly as well. We humans owe much of our versatility and athleticism to our prehensile hands and flexible limbs, but these also make us prone to sprains, torn ligaments, and dislocations: Structural reinforcement has been compromised for agility. Organisms face many such *trade-offs* in which the ability to perform one function may reduce the ability to perform another—and as with seals and humans, those trade-offs can restrict adaptive evolution.

▼ Figure 23.19 Lack of variation in a population can limit adaptation. For the snowshoe hare, changing its coat color from brown **(a)** to white **(b)** too early is disadvantageous, but the population lacks alleles that would encode a delay in molting.

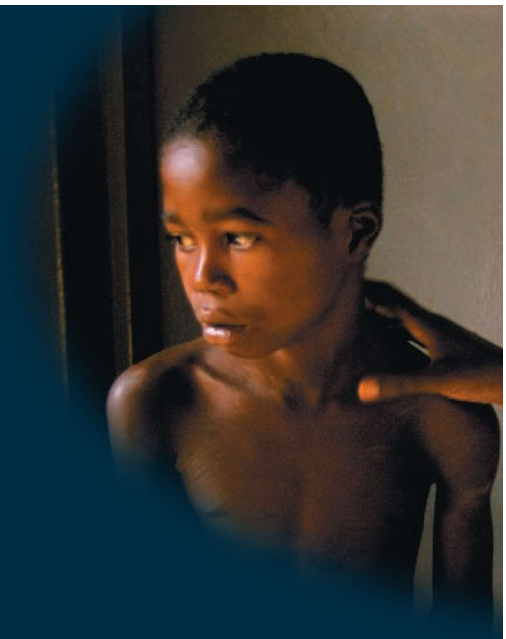




▼ **Figure 23.18**

MAKE CONNECTIONS

The Sickle-Cell Allele



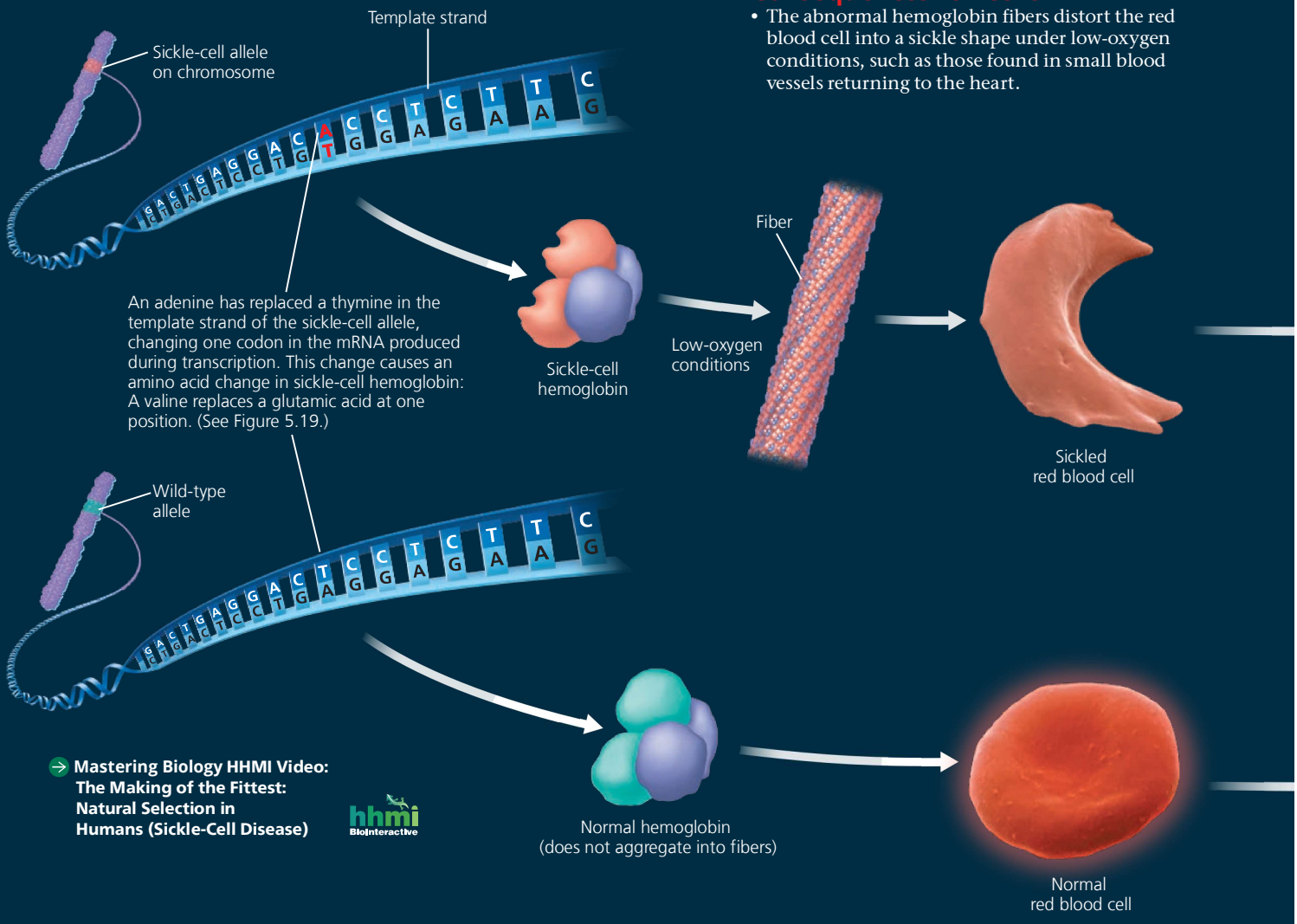
This child has sickle-cell disease, a genetic disorder that strikes individuals who have two copies of the sickle-cell allele. This allele causes an abnormality in the structure and function of hemoglobin, the oxygen-carrying protein in red blood cells. Although sickle-cell disease is lethal if not treated, in some regions the sickle-cell allele can reach frequencies as high as 15–20%. How can such a harmful allele be so common?

Events at the Molecular Level

- Due to a point mutation, the sickle-cell allele differs from the wild-type allele by a single nucleotide. (See Figure 17.26.)
- The resulting change in one amino acid leads to hydrophobic interactions between the sickle-cell hemoglobin proteins under low-oxygen conditions.
- As a result, the sickle-cell proteins bind to each other in chains that together form a fiber.

Consequences for Cells

- The abnormal hemoglobin fibers distort the red blood cell into a sickle shape under low-oxygen conditions, such as those found in small blood vessels returning to the heart.



Mastering Biology HHMI Video: The Making of the Fittest: Natural Selection in Humans (Sickle-Cell Disease)





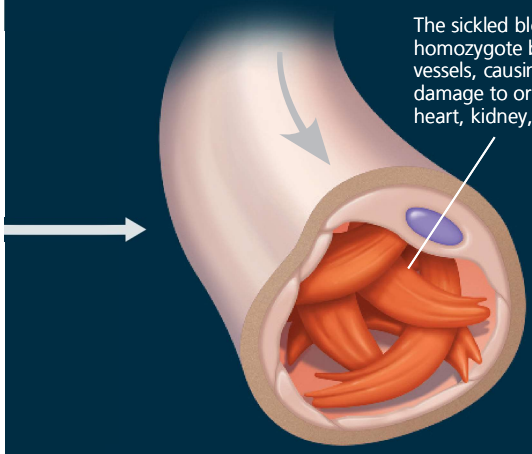
Infected mosquitoes spread malaria when they bite people. (See Figure 28.16.)

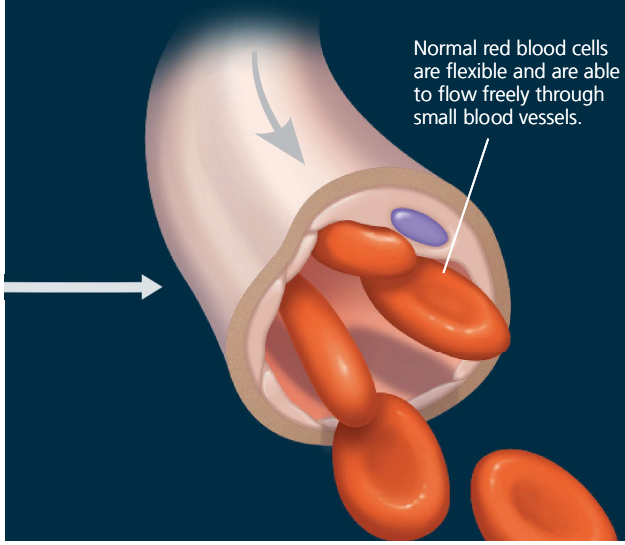
Effects on Individual Organisms

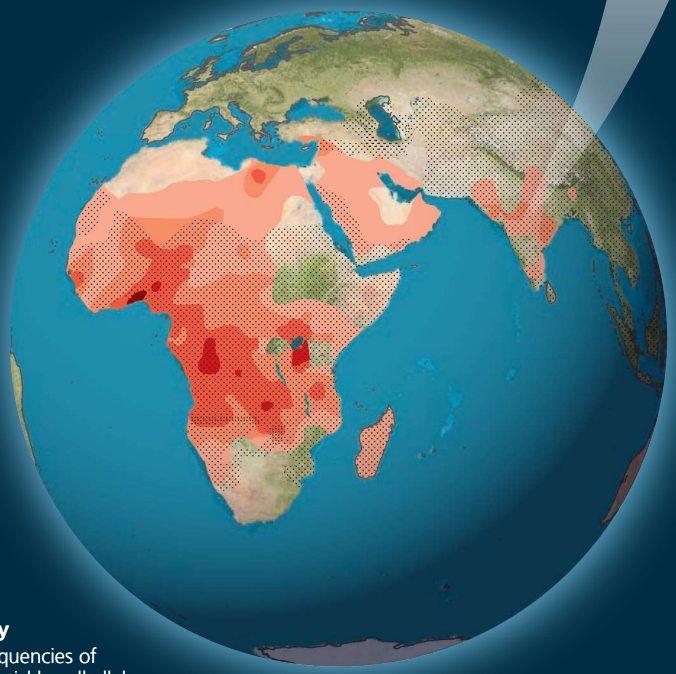
- The formation of sickled red blood cells causes homozygotes with two copies of the sickle-cell allele to have sickle-cell disease.
- Some sickling also occurs in heterozygotes, but not enough to cause the disease; they have sickle-cell trait. (See Figure 14.17.)

Evolution in Populations

- Homozygotes with two sickle-cell alleles are strongly selected against because of mortality caused by sickle-cell disease. In contrast, heterozygotes experience few harmful effects from sickling yet are more likely to survive malaria than are homozygotes.
- In regions where malaria is common, the net effect of these opposing selective forces is heterozygote advantage. This has caused evolutionary change in populations—the products of which are the areas of relatively high frequencies of the sickle-cell allele shown in the map.







Key

Frequencies of the sickle-cell allele

- 3.0–6.0%
- 6.0–9.0%
- 9.0–12.0%
- 12.0–15.0%
- >15.0%

Distribution of malaria caused by *Plasmodium falciparum* (a parasitic unicellular eukaryote carried by mosquitoes)

MAKE CONNECTIONS

In a region free of malaria, would individuals who are heterozygous for the sickle-cell allele be selected for or selected against? Explain.

4. **Chance, natural selection, and the environment interact.** Chance events can affect the subsequent evolutionary history of populations. For instance, when a storm blows insects or birds hundreds of kilometers over an ocean to an island, the wind does not necessarily transport those individuals that are best suited to the new environment. Thus, not all alleles present in the founding population's gene pool are better suited to the new environment than the alleles that are "left behind." In addition, the environment at a particular location may change unpredictably from year to year, again limiting the extent to which adaptive evolution results in organisms being well suited for current environmental conditions.

With these four constraints, evolution does not result in perfect organisms. Natural selection operates on a "better than" basis. We can, in fact, see evidence for evolution in the many imperfections of the organisms it produces.

CONCEPT CHECK 23.4

1. What is the relative fitness of a sterile mule? Explain.
2. Explain why natural selection is the only mechanism that consistently leads to adaptive evolution in a population.
3. **VISUAL SKILLS** Consider a population in which heterozygotes at a certain locus have an extreme phenotype (such as being larger than homozygotes) that confers a selective advantage. Compare this description to the three types of selection shown in Figure 23.13. Does this situation represent directional, disruptive, or stabilizing selection? Explain.

For suggested answers, see Appendix A.

23 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

CONCEPT 23.1

Genetic variation makes evolution possible *(pp. 487–489)*

- **Genetic variation** refers to genetic differences among individuals within a population.
- The nucleotide differences that provide the basis of genetic variation originate when mutation and gene duplication produce new alleles and new genes. New genetic variants are produced rapidly in organisms with short generation times. In sexually reproducing organisms, most of the genetic differences among individuals result from crossing over, the independent assortment of chromosomes, and fertilization.

? *Typically, most of the nucleotide variability that occurs within a genetic locus does not affect the phenotype. Explain why.*

CONCEPT 23.2

The Hardy-Weinberg equation can be used to test whether a population is evolving *(pp. 489–493)*

- A **population**, a localized group of organisms belonging to one species, is united by its **gene pool**, the aggregate of all the alleles in the population.
- For a population in **Hardy-Weinberg equilibrium**, the allele and genotype frequencies will remain constant if the population is large, mating is random, mutation is negligible, there is no gene flow, and there is no natural selection. For such a population, if p and q represent the frequencies of the only two possible alleles at a particular locus, then p^2 is the frequency of one kind of homozygote, q^2 is the frequency of the other kind of homozygote, and $2pq$ is the frequency of the heterozygous genotype.

? *Is it circular reasoning to calculate* p *and* q *from observed genotype frequencies and then use those values of* p *and* q *to test if the population is in Hardy-Weinberg equilibrium? Explain your answer.*

CONCEPT 23.3

Natural selection, genetic drift, and gene flow can alter allele frequencies in a population *(pp. 493–497)*

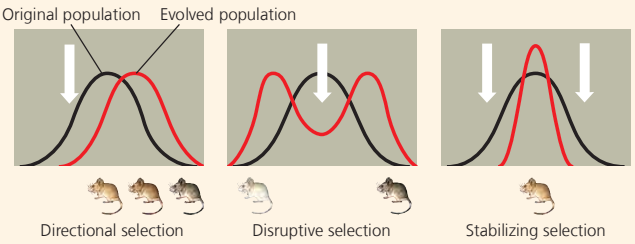
- In natural selection, individuals that have certain inherited traits tend to survive and reproduce at higher rates than other individuals *because of* those traits.
- In **genetic drift**, chance fluctuations in allele frequencies over generations tend to reduce genetic variation.
- **Gene flow**, the transfer of alleles between populations, tends to reduce genetic differences between populations over time.

? *Would two small, geographically isolated populations in very different environments be likely to evolve in similar ways? Explain.*

CONCEPT 23.4

Natural selection is the only mechanism that consistently causes adaptive evolution *(pp. 497–504)*

- One organism has greater **relative fitness** than another organism if it leaves more fertile descendants. The modes of natural selection differ in their effect on phenotype:



- Unlike genetic drift and gene flow, natural selection consistently increases the frequencies of alleles that enhance survival and reproduction, thus improving the degree to which organisms are well-suited for life in their environment.
- **Sexual selection** can result in secondary sex characteristics that can give individuals advantages in mating.
- **Balancing selection** occurs when natural selection maintains two or more forms in a population.

- There are constraints to evolution: Natural selection can act only on available variation; structures result from modified ancestral anatomy; adaptations are often compromises; and chance, natural selection, and the environment interact.

? *How might secondary sex characteristics in males differ from those in females in a species in which females compete for mates?*

TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

1. Natural selection changes allele frequencies because some _____ survive and reproduce better than others.
(A) alleles (C) species
(B) loci (D) individuals

2. No two people are genetically identical, except for identical twins. The main source of genetic variation among humans is
(A) new mutations that occurred in the preceding generation.
(B) genetic drift.
(C) the reshuffling of alleles in sexual reproduction.
(D) environmental effects.

Levels 3-4: Applying/Analyzing

3. If the nucleotide variability of a locus equals 0%, what is the gene variability and number of alleles at that locus?
(A) gene variability = 0%; number of alleles = 0
(B) gene variability = 0%; number of alleles = 1
(C) gene variability = 0%; number of alleles = 2
(D) gene variability > 0%; number of alleles = 2

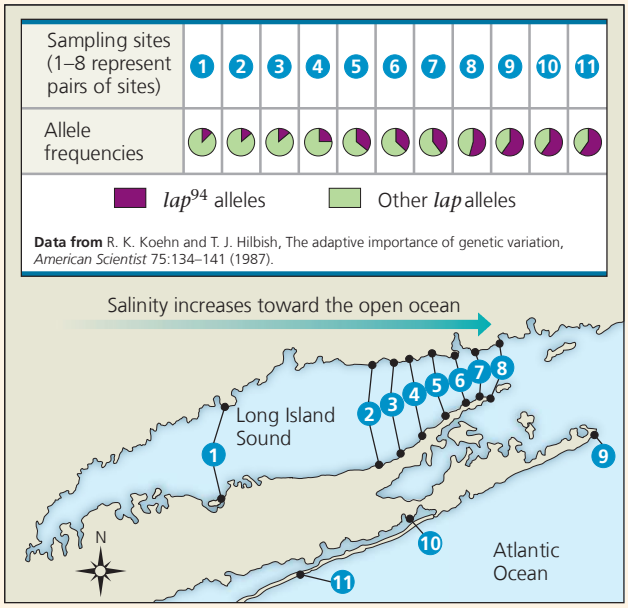
4. One population of a species has 25 individuals, all with genotype *AA*; a second population of this species has 40 individuals, all with genotype *aa*. Assume that these populations live far apart but in similar environmental conditions. Based on this information, the observed genetic variation most likely resulted from
(A) genetic drift. (C) nonrandom mating.
(B) gene flow. (D) directional selection.

5. A fruit fly population has a gene with two alleles, *A1* and *A2*. Tests show that 70% of the gametes produced in the population contain the *A1* allele. If the population is in Hardy-Weinberg equilibrium, what proportion of the flies carry both *A1* and *A2*?
(A) 0.7 (B) 0.49 (C) 0.42 (D) 0.21

Levels 5-6: Evaluating/Creating

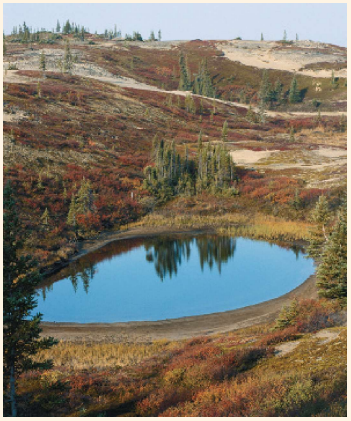
6. **EVOLUTION CONNECTION** Using at least two examples, explain how the process of evolution is revealed by the imperfections of living organisms.

7. **SCIENTIFIC INQUIRY • INTERPRET THE DATA** For populations of the marine mussel *Mytilus edulis* around Long Island, New York, researchers measured the frequency of a particular allele (lap^{94}) for an enzyme involved in regulating the mussel's saltwater balance. They presented their data as a series of pie charts linked to sampling sites within Long Island Sound, where the salinity is highly variable, and along the coast of the open ocean, where salinity is constant. (a) Create a data table for the 11 sampling sites by estimating the frequency of lap^{94} from the pie charts. (b) Graph the frequencies for sites 1–8 to show how the frequency of this allele changes with increasing salinity in Long Island Sound (from southwest to northeast). Evaluate how the data from sites 9–11 compare with the data from the sites within the Sound. (c) Considering the various mechanisms that can alter allele frequency, construct a hypothesis that explains the patterns in the data and that accounts for the following observations: (1) The lap^{94} allele helps mussels maintain osmotic balance in water with a high salt concentration but is costly to use in less salty water; and (2) mussels produce larvae that can disperse long distances before they settle on rocks and grow into adults.



8. **WRITE ABOUT A THEME: ORGANIZATION** Heterozygotes at the sickle-cell locus produce both normal and abnormal (sickle-cell) hemoglobin (see Concept 14.4). When hemoglobin molecules are packed into a heterozygote's red blood cells, some cells receive relatively large quantities of abnormal hemoglobin, making these cells prone to sickling. In a short essay (approximately 100–150 words), explain how these molecular and cellular events lead to emergent properties at the individual and population levels of biological organization.

9. **SYNTHESIZE YOUR KNOWLEDGE**



The lake shown in this photograph, called a kettle lake, formed 14,000 years ago when a glacier that covered the surrounding area melted. Initially devoid of animal life, over time the lake was colonized by invertebrates and other animals. Hypothesize how mutation, natural selection, genetic drift, and gene flow may have affected populations that colonized the lake.

For selected answers, see Appendix A.

Explore Scientific Papers with Science in the Classroom AAAS
How does a native species evolve in response to an introduced species? Go to "There's a New Kid in Town" at www.scienceintheclassroom.org.
Instructors: Questions can be assigned in Mastering Biology.

24 The Origin of Species

KEY CONCEPTS

24.1 The biological species concept emphasizes reproductive isolation *p. 507*

24.2 Speciation can take place with or without geographic separation *p. 511*

24.3 Hybrid zones reveal factors that cause reproductive isolation *p. 516*

24.4 Speciation can occur rapidly or slowly and can result from changes in few or many genes *p. 520*

Study Tip

Make a table: Some processes that can lead to speciation only occur in allopatric (geographically separated) populations, while others also occur in sympatric (geographically overlapping) populations. To help you keep track of these processes and the geographic conditions under which they can occur, fill in the table as you read the chapter.

Process (include page # or figure #)	Can occur in allopatric populations (yes/no)?	Can occur in sympatric populations (yes/no)?
Sexual selection (Figure 24.12)	Yes	Yes

Go to Mastering Biology

For Students (in eText and Study Area)
- Get Ready for Chapter 24
- Figure 24.10 Walkthrough: One Mechanism for Allopolyploid Speciation in Plants

For Instructors to Assign (in Item Library)
- Interpreting Data: Evolution of Reproductive Barriers in Lab Populations of Fruit Flies
- Problem-Solving Exercise: Is Hybridization Promoting Insecticide Resistance?

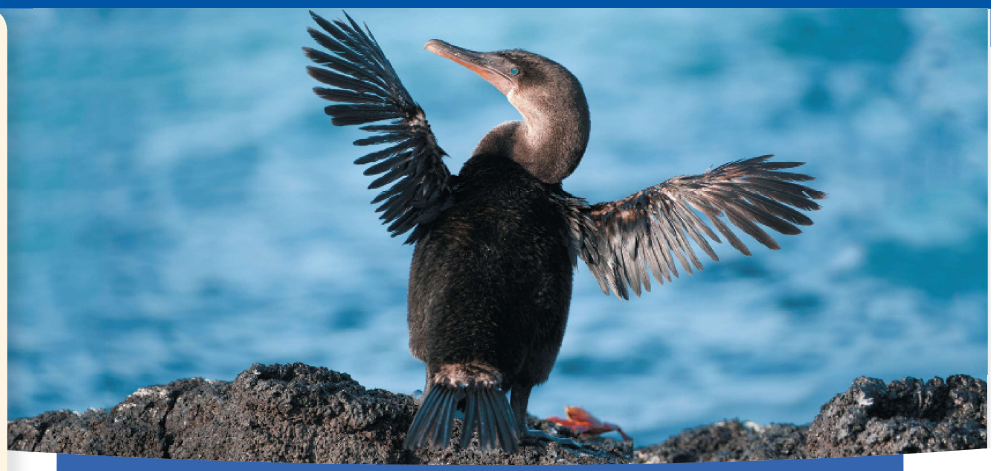
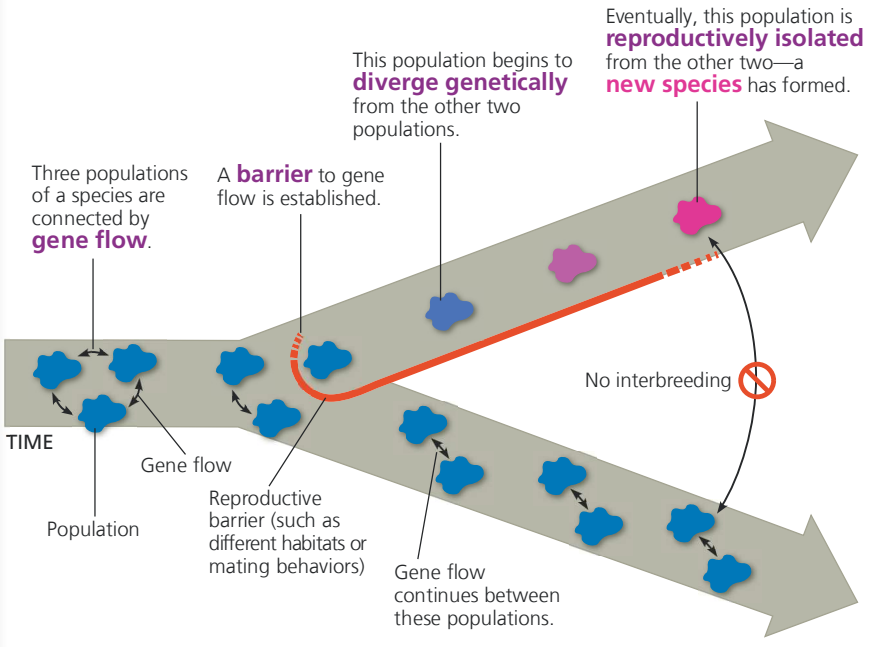


Figure 24.1 This flightless cormorant is one of many species in the Galápagos Islands that are found nowhere else in the world. How did a bird that cannot fly come to live in this isolated place? When Darwin visited the Galápagos, he also was intrigued by its unique species, and later concluded that they must have originated in the islands from ancestors that had traveled from South America.

How do new species originate from existing species?

Over time, populations of a single species connected by gene flow can diverge genetically, giving rise to a new species:



When Darwin came to the Galápagos Islands, he noted that they were teeming with unique species, like the flightless bird in Figure 24.1. Later, he realized that these species had formed relatively recently, writing in his diary, "Both in space and time, we seem to be brought somewhat near to that great fact—that mystery of mysteries—the first appearance of new beings on this Earth."

The "mystery of mysteries" that captivated Darwin is **speciation**, the process by which one species splits into two species. Speciation fascinated Darwin (and many biologists since) because it has produced the tremendous diversity of life, repeatedly yielding new species that differ from existing ones. Speciation also helps to explain the many features that organisms share (the unity of life): When one species splits into two, the species that result share many characteristics because they are descended from this common ancestor. For example, at the DNA sequence level, such similarities indicate that the flightless cormorant in Figure 24.1 is closely related to flying cormorants found in the Americas. This suggests that the flightless cormorant originated from an ancestral cormorant species that flew from the mainland to the Galápagos.

Speciation forms a conceptual bridge between **microevolution**, changes over time in allele frequencies in a population, and **macroevolution**, the broad pattern of evolution above the species level. An example of macroevolutionary change is the origin of new groups of organisms, such as mammals or flowering plants, through a series of speciation events. We examined microevolutionary mechanisms in Chapter 23, and we'll turn to macroevolution in Chapter 25. In this chapter, we'll explore the mechanisms by which new species originate from existing ones. First, let's establish what we actually mean by a "species."

▼ Figure 24.2 The biological species concept is based on the potential to interbreed, not on physical similarity.



(a) Similarity between different species. The eastern meadowlark (*Sturnella magna*, left) and the western meadowlark (*Sturnella neglecta*, right) have similar body shapes and colorations. Nevertheless, they are distinct biological species because their songs and other behaviors are different enough to prevent interbreeding should they meet in the wild.



(b) Diversity within a species. As diverse as we may be in appearance, all humans belong to a single biological species (*Homo sapiens*), defined by our capacity to interbreed successfully.

CONCEPT 24.1

The biological species concept emphasizes reproductive isolation

The word *species* is Latin for "kind" or "appearance." In daily life, we commonly distinguish between various "kinds" of organisms—dogs and cats, for instance—based on differences in their appearance. But are organisms truly divided into the discrete units we call species? To answer this question, biologists compare not only the morphology (body form) of different groups of organisms but also their physiology, biochemistry, and DNA sequences. The results generally confirm that morphologically distinct species are indeed discrete groups, differing in many ways besides their body forms.

The Biological Species Concept

The primary definition of species used in this textbook is the **biological species concept**. According to this concept, a **species** is a group of populations whose members have the potential to interbreed in nature and produce viable, fertile offspring—but do not produce viable, fertile offspring with members of other such groups **(Figure 24.2)**. Thus, the members of a biological species are united by being reproductively compatible, at least potentially. All human beings, for example, belong to the same species. A businesswoman in Manhattan may be unlikely to meet a dairy farmer in Mongolia, but if the two should happen to meet and mate, they could have viable babies who develop into fertile adults. In contrast, humans and chimpanzees remain distinct biological species, even where they live in the same region, because many factors keep them from interbreeding and producing fertile offspring.

What holds the gene pool of a species together, causing its members to resemble each other more than they resemble members of other species? Recall the evolutionary mechanism of *gene flow*, the transfer of alleles between populations

(see Concept 23.3). Typically, gene flow occurs between the different populations of a species. This ongoing exchange of alleles tends to hold the populations together genetically. But as we'll explore in this chapter, a reduction or lack of gene flow can play a key role in the formation of new species.

Reproductive Isolation

Because biological species are defined in terms of reproductive compatibility, the formation of a new species hinges on **reproductive isolation**—the existence of biological

▼ Figure 24.3 Exploring Reproductive Barriers

Prezygotic barriers impede mating or hinder fertilization if mating does occur

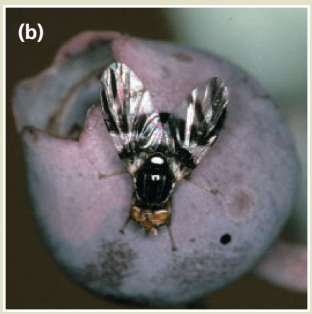


Habitat Isolation

Two species that occupy different habitats within the same area may encounter each other rarely, if at all.

Example: These two fly species in the genus *Rhagoletis* occur in the same geographic areas, but the apple maggot fly (*Rhagoletis pomonella*) feeds and mates on hawthorns and apples **(a)** while its close relative, the blueberry maggot fly (*R. mendax*), mates and lays its eggs only on blueberries **(b)**.





Temporal Isolation

Species that breed during different times of the day, different seasons, or different years cannot mix their gametes.

Example: In North America, the geographic ranges of the western spotted skunk (*Spilogale gracilis*) **(c)** and the eastern spotted skunk (*Spilogale putorius*) **(d)** overlap, but *S. gracilis* mates in late summer and *S. putorius* mates in late winter.





Behavioral Isolation

Courtship rituals that attract mates and other behaviors unique to a species are effective reproductive barriers, even between closely related species.

Example: Blue-footed boobies, inhabitants of the Galápagos, mate only after a courtship display unique to their species. Part of the "script" calls for the male to high-step **(e)**, a behavior that calls the female's attention to his bright blue feet.



Mastering Biology **Video: Blue-Footed Boobies Courtship Ritual**

Mechanical Isolation

Mating is attempted, but morphological differences prevent its successful completion.

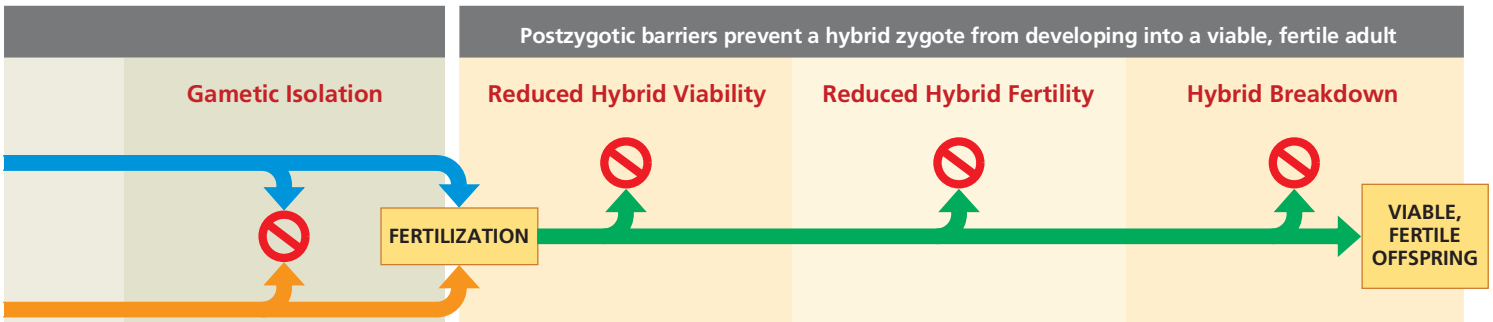
Example: Snails in the genus *Bradybaena* approach each other headfirst when they attempt to mate. Once their heads have moved slightly past each other, the snails' genitals emerge, and if their shells spiral in the same direction, mating can occur **(f)**. But if a snail attempts to mate with a snail whose shell spirals in the opposite direction **(g)**, the two snails' genital openings (indicated by arrows) will not be aligned, and mating cannot be completed.





factors (barriers) that impede members of two species from interbreeding and producing viable, fertile offspring **(Figure 24.3)**. Such barriers block gene flow between the species and limit the formation of **hybrids**, offspring that result from an interspecific mating. Although a single barrier may not prevent all gene flow, a combination of several barriers can effectively isolate a species' gene pool.

Clearly, a fly cannot mate with a frog or a fern, but the reproductive barriers between more closely related species are not so obvious. As described in Figure 24.3, these barriers can be



Gametic Isolation

Sperm of one species may not be able to fertilize the eggs of another species. For instance, sperm may not be able to survive in the reproductive tract of females of the other species, or biochemical mechanisms may prevent the sperm from penetrating the membrane surrounding the other species' eggs.

Example: Gametic isolation separates certain closely related species of aquatic animals, such as sea urchins **(h)**. Sea urchins release their sperm and eggs into the surrounding water, where they fuse and form zygotes. It is difficult for gametes of different species, such as the red and purple urchins shown here (*Strongylocentrotus franciscanus* and *S. purpuratus*, respectively), to fuse because proteins on the surfaces of the eggs and sperm bind very poorly to each other.



Reduced Hybrid Viability

The genes of different parent species may interact in ways that impair the hybrid's development or survival in its environment.

Example: Some salamander subspecies of the genus *Ensatina* live in the same regions and habitats, where they may occasionally hybridize. But most of the hybrids do not complete development, and those that do are frail **(i)**.



Reduced Hybrid Fertility

Even if hybrids are vigorous, they may be sterile. If the chromosomes of the two parent species differ in number or structure, meiosis in the hybrids may fail to produce normal gametes. Since the infertile hybrids cannot produce offspring when they mate with either parent species, genes cannot flow freely between the species.

Example: The hybrid offspring of a male donkey **(j)** and a female horse **(k)** is a mule **(l)**, which is robust but sterile. A "hinny" (not shown), the offspring of a female donkey and a male horse, is also sterile.







Hybrid Breakdown

Some first-generation hybrids are viable and fertile, but when they mate with one another or with either parent species, offspring of the next generation are feeble or sterile.

Example: Strains of cultivated rice have accumulated different mutant recessive alleles at two loci in the course of their divergence from a common ancestor. Hybrids between them are vigorous and fertile (**m**, left and right), but plants in the next generation that carry too many of these recessive alleles are small and sterile (**m**, center). Although these rice strains are not yet considered different species, they have begun to be separated by postzygotic barriers.



classified according to whether they contribute to reproductive isolation before or after fertilization. **Prezygotic barriers** ("before the zygote") block fertilization from occurring. Such barriers typically act in one of three ways: by impeding members of different species from attempting to mate, by preventing an attempted mating from being completed successfully, or by hindering fertilization if mating is completed successfully. If a sperm cell from one species overcomes prezygotic barriers and fertilizes an ovum from another species, a variety of **postzygotic barriers** ("after the zygote") may contribute to reproductive isolation after the hybrid zygote is formed. Developmental errors may reduce survival among hybrid embryos. Or problems after birth may cause hybrids to be infertile or decrease their chance of surviving long enough to reproduce.

Mastering Biology Video: Prezygotic Barriers to Mating in Galápagos Finches by Peter and Rosemary Grant

Limitations of the Biological Species Concept

One strength of the biological species concept is that it directs our attention to a way by which speciation can occur: by the evolution of reproductive isolation. However, the number of species to which this concept can be usefully applied is limited. There is, for example, no way to evaluate the reproductive isolation of fossils. The biological species concept also does not apply to organisms that reproduce asexually all or most of the time, such as prokaryotes. (Many prokaryotes do transfer genes among themselves, as we will discuss in Concept 27.2, but this is not part of their reproductive process.) Furthermore, in the biological species concept, species are designated by the *absence* of gene flow. But there are many pairs of species that are morphologically and ecologically distinct, and yet gene flow occurs between them. An example is the grizzly bear (*Ursus arctos*) and polar bear (*Ursus maritimus*), whose hybrid offspring have been dubbed "grolar bears" **(Figure 24.4)**. As we'll discuss, natural selection can cause such species to remain distinct even though some gene flow occurs between them. Because of the limitations to the biological species concept, alternative species concepts are useful in certain situations.

Other Definitions of Species

While the biological species concept emphasizes the *separateness* of different species due to reproductive barriers, several other definitions emphasize the *unity within* a species. For example, the **morphological species concept** distinguishes a species by body shape and other structural features. The morphological species concept can be applied to asexual and sexual organisms, and it can be useful even without information on the extent of gene flow. In practice, scientists often distinguish species using morphological criteria. A disadvantage of this approach, however, is that it relies on subjective criteria; researchers may disagree on which structural features distinguish a species.



▲ Figure 24.4 Hybridization between two species of bears in the genus *Ursus*.

The **ecological species concept** defines a species in terms of its ecological niche, the sum of how members of the species interact with the nonliving and living parts of their environment (see Concept 54.1). For example, two species of oak trees might differ in their size or in their ability to tolerate dry conditions, yet still occasionally interbreed. Because they occupy different ecological niches, these oaks would be considered separate species even though they are connected by some gene flow. Unlike the biological species concept, the ecological species concept can accommodate asexual as well as sexual species. It also emphasizes the role of disruptive natural selection as organisms adapt to different environments.

In addition to those discussed here, more than 20 other species definitions have been proposed. The usefulness of each definition depends on the situation and the research questions being asked. For our purposes of studying how species originate, the biological species concept, with its focus on reproductive barriers, is particularly helpful.

Mastering Biology HHMI Video: The Origin of Species: The Beak of the Finch

CONCEPT CHECK 24.1

1. (a) Which species concept(s) could you apply to both asexual and sexual species? (b) Which would be most useful for identifying species in the field? Explain.
2. **WHAT IF?** Suppose two bird species live in a forest and are not known to interbreed. One species feeds and mates in the treetops and the other on the ground. But in captivity, the birds can interbreed and produce viable, fertile offspring. What type of reproductive barrier most likely keeps these species separate in nature? Explain.

For suggested answers, see Appendix A.

CONCEPT 24.2

Speciation can take place with or without geographic separation

Having discussed what constitutes a unique species, let's return to the process by which such species arise from existing species. We'll describe this process by focusing on the geographic setting in which gene flow is interrupted between populations of the existing species—in allopatric speciation the populations are geographically isolated, while in sympatric speciation they are not **(Figure 24.5)**.

Allopatric ("Other Country") Speciation

In **allopatric speciation** (from the Greek *allos*, other, and *patra*, homeland), gene flow is interrupted when a population is divided into geographically isolated subpopulations. For example, the water level in a lake may subside, resulting in two or more smaller lakes that are now home to separated populations (see Figure 24.5a). Or a river may change course and divide a population of animals that cannot cross it. Allopatric speciation can also occur without geologic change, such as when individuals colonize a remote area and their descendants become geographically isolated from the parent population. The flightless cormorant shown in Figure 24.1 probably originated in this way from an ancestral flying species that reached the Galápagos Islands.

The Process of Allopatric Speciation

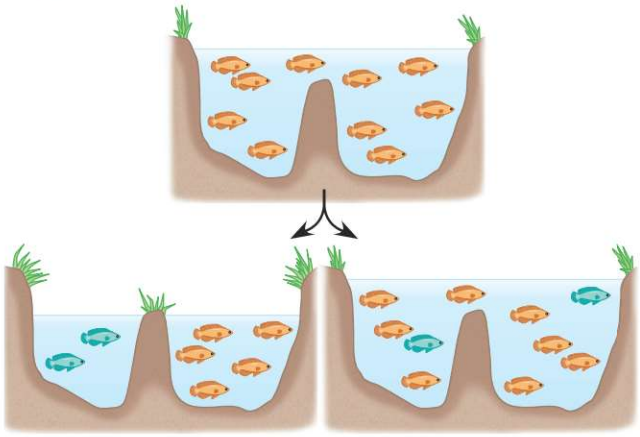
How formidable must a geographic barrier be to promote allopatric speciation? The answer depends on the ability of the organisms to move about. Birds, mountain lions, and coyotes can cross rivers and canyons—as can windblown pollen and the seeds of some flowering plants. In contrast, small rodents may find a river or canyon a formidable barrier.

Once geographic isolation has occurred, the separated gene pools may diverge. Different mutations arise, and natural selection and genetic drift may alter allele frequencies in different ways in the separated populations. Reproductive isolation may then evolve as a by-product of the genetic divergence that results from selection or drift.

Figure 24.6 describes an example. On Andros Island, in the Bahamas, populations of the mosquitofish *Gambusia hubbsi* colonized a series of ponds that later became isolated from one another. Genetic analyses indicate that little or no gene flow currently occurs between the ponds. The environments of these ponds are very similar except that some contain predatory fishes, while others do not. In ponds with predatory fishes, selection has favored the evolution of a mosquitofish body shape that enables rapid bursts of speed (see Figure 24.6a). In ponds without predatory fishes, selection has favored a different body shape, one that improves the ability to swim for long periods of time (see Figure 24.6b).

How have these different selective pressures affected the evolution of reproductive barriers? Researchers studied this question by bringing together mosquitofish from the two types of ponds. They found that female mosquitofish prefer to mate with males whose body shape is similar to their own. This preference establishes a behavioral barrier

▼ Figure 24.5 The geography of speciation.



(a) Allopatric speciation. A population forms a new species while geographically isolated from its parent population.

(b) Sympatric speciation. A subset of a population forms a new species without geographic separation.

▼ Figure 24.6 Evolution in mosquitofish populations. Different body shapes have evolved in mosquitofish populations from ponds with and without predators. These differences affect how quickly the fishes can accelerate to escape and their survival rate when exposed to predators.

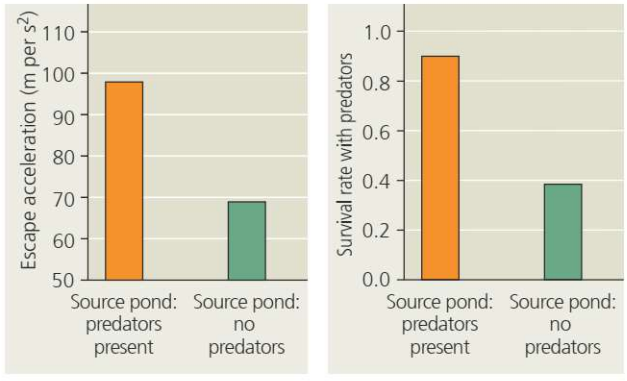


In ponds with predatory fishes, the mosquitofish's head is streamlined and the tail is powerful, enabling rapid bursts of speed.



In ponds without predatory fishes, mosquitofish have a different body shape that favors long, steady swimming.

(a) Differences in body shape



(b) Differences in escape acceleration and survival

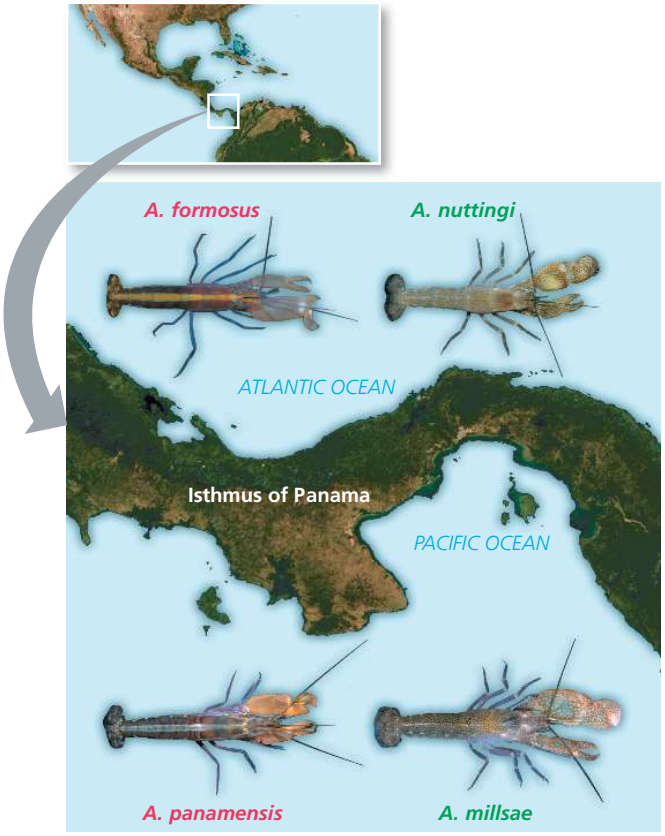
to reproduction between mosquitofish from ponds with predators and those from ponds without predators. Thus, as a by-product of selection for avoiding predators, reproductive barriers have formed in these allopatric populations.

Evidence of Allopatric Speciation

Many studies provide evidence that speciation can occur in allopatric populations. For example, laboratory studies show that reproductive barriers can develop when populations are isolated experimentally and subjected to different environmental conditions **(Figure 24.7)**.

Field studies indicate that allopatric speciation also can occur in nature. Consider the 30 species of snapping shrimp in the genus *Alpheus* that live off the Isthmus of Panama, the land bridge that connects South and North America **(Figure 24.8)**. Fifteen of these species live on the Atlantic side of the isthmus, while the other 15 live on the Pacific side. Before the isthmus formed, gene flow could occur between the Atlantic and Pacific populations of snapping shrimp. Did the species on different sides of the isthmus originate by allopatric speciation? Morphological and genetic data group these shrimp into 15 pairs of *sister species*, pairs whose member species are each other's closest relative. In each of these

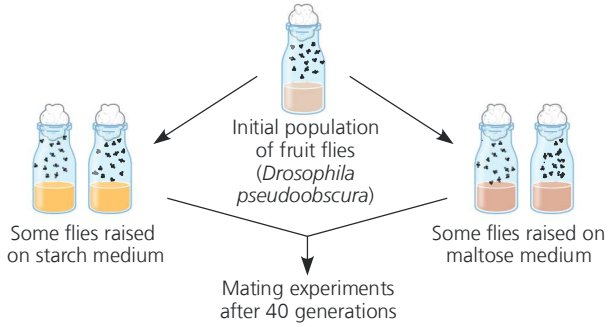
▼ Figure 24.8 Allopatric speciation in snapping shrimp (*Alpheus*). The shrimp pictured are just 2 of the 15 pairs of sister species that arose as populations were divided by the formation of the Isthmus of Panama. The color-coded type indicates the sister species.



▼ Figure 24.7 Inquiry

Can divergence of allopatric populations lead to reproductive isolation?

Experiment A researcher divided a laboratory population of the fruit fly *Drosophila pseudoobscura*, raising some flies on a starch medium and others on a maltose medium. After one year (about 40 generations), natural selection resulted in divergent evolution: Populations raised on starch digested starch more efficiently, while those raised on maltose digested maltose more efficiently. The researcher then put flies from the same or different populations in mating cages and measured mating frequencies. All flies used in the mating preference tests were reared for one generation on a standard cornmeal medium.



Results Mating patterns among populations of flies raised on different media are shown below. When flies from "starch populations" were mixed with flies from "maltose populations," the flies tended to mate with like partners (see the lefthand table). But in a control group consisting of flies from two different populations adapted to starch, the flies were about as likely to mate with flies of the other population as with flies of their own population (see the righthand table); similar results were obtained for control groups adapted to maltose.

		Female	
		Starch	Maltose
Male	Starch	22	9
	Maltose	8	20

Number of matings in experimental group

		Female	
		Starch population 1	Starch population 2
Male	Starch population 1	18	15
	Starch population 2	12	15

Number of matings in control group

Conclusion In the experimental group, the strong preference of "starch flies" and "maltose flies" to mate with like-adapted flies indicates that a reproductive barrier was forming between these fly populations. Although this barrier was not absolute (some mating between starch flies and maltose flies did occur), after 40 generations reproductive isolation appeared to be increasing. This barrier may have been caused by differences in courtship behavior that arose as an incidental by-product of differing selective pressures as these allopatric populations adapted to different sources of food.

Data from D. M. B. Dodd, Reproductive isolation as a consequence of adaptive divergence in *Drosophila pseudoobscura*, *Evolution* 43:1308–1311 (1989).

WHAT IF? *Why were all flies used in the mating preference tests reared on a standard medium (rather than on starch or maltose)?*

15 pairs, one of the sister species lives on the Atlantic side of the isthmus, while the other lives on the Pacific side. This fact strongly suggests that the two species arose as a consequence of geographic separation. Furthermore, genetic analyses indicate that the *Alpheus* species originated from 9 to 3 million years ago, with the sister species that live in the deepest water diverging first. These divergence times are consistent with geologic evidence that the isthmus formed gradually, starting 10 million years ago, and closing completely about 3 million years ago.

The importance of allopatric speciation is also suggested by the fact that regions that are isolated or highly subdivided by barriers typically have more species than do otherwise similar regions that lack such features. For example, many unique plants and animals are found on the geographically isolated Hawaiian Islands (we'll return to the origin of Hawaiian species in Concept 25.4). Field studies also show that reproductive isolation between two populations generally increases as the geographic distance between them increases, a finding consistent with allopatric speciation. In the **Scientific Skills Exercise**, you can analyze data from one such study that examined reproductive isolation in geographically separated salamander populations.

Note that while geographic isolation prevents interbreeding between members of allopatric populations, physical separation is not a biological barrier to reproduction. Biological reproductive barriers such as those described in Figure 24.3 are intrinsic to the organisms themselves. Hence, it is biological barriers that can prevent interbreeding when members of different populations come into contact with one another.

Sympatric ("Same Country") Speciation

In **sympatric speciation** (from the Greek *syn*, together), speciation occurs in populations that live in the same geographic area (see Figure 24.5b). How can reproductive barriers form between sympatric populations while their members remain in contact with each other? Although such contact (and the ongoing gene flow that results) makes sympatric speciation less common than allopatric speciation, sympatric speciation can occur if gene flow is reduced by such factors as polyploidy, sexual selection, and habitat differentiation. (Note that sexual selection and habitat differentiation also can promote allopatric speciation.)

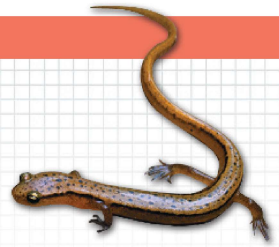
Scientific Skills Exercise

Identifying Independent and Dependent Variables, Making a Scatter Plot, and Interpreting Data

Does Distance Between Salamander Populations Increase Their Reproductive Isolation? Allopatric speciation begins when populations become geographically isolated, reducing mating between individuals in different populations and thus reducing gene flow. It is logical that as distance between populations increases, so will their degree of reproductive isolation. To test this hypothesis, researchers studied populations of the dusky salamander (*Desmognathus ochrophaeus*) living on different mountain ranges in the southern Appalachians.

How the Experiment Was Done The researchers tested the reproductive isolation of pairs of salamander populations by leaving one male and one female together and later checking the females for the presence of sperm. Four mating combinations were tested for each pair of populations (A and B)—two *within* the same population (female A with male A and female B with male B) and two *between* populations (female A with male B and female B with male A).

Data from the Experiment The researchers used an index of reproductive isolation that ranged from a value of 0 (no isolation) to a value of 2 (full isolation). The proportion of successful matings for each mating combination was measured, with 100% success = 1 and no success = 0. The reproductive isolation value for two populations is the sum of the proportion of successful matings of each type within populations (AA + BB) minus the sum of the proportion of successful matings of each type between populations (AB + BA). The table provides distance and reproductive isolation data for 27 pairs of dusky salamander populations.



INTERPRET THE DATA

1. State the researchers' hypothesis, and identify the independent and dependent variables in this study. Explain why the researchers used four mating combinations for each pair of populations.
2. Calculate the value of the reproductive isolation index **(a)** if *all* of the matings within a population were successful, but *none* of the matings between populations were successful; **(b)** if salamanders are equally successful in mating with members of their own population and members of another population.
3. Make a scatter plot to help you visualize any patterns that might indicate a relationship between the variables. Plot the independent variable on the *x*-axis and the dependent variable on the *y*-axis. (For additional information about graphs, see the Scientific Skills Review in Appendix D.)
4. Interpret your graph by **(a)** explaining in words any pattern indicating a possible relationship between the variables and **(b)** hypothesizing the possible cause of such a relationship.

Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

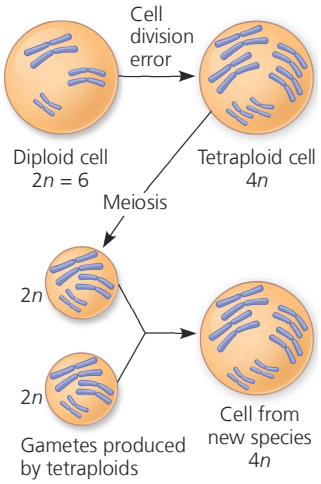
Data from S. G. Tilley, A. Verrell, and S. J. Arnold, Correspondence between sexual isolation and allozyme differentiation: a test in the salamander *Desmognathus ochrophaeus*, *Proceedings of the National Academy of Sciences USA* 87:2715–2719 (1990).

Geographic Distance (km)	15	32	40	47	42	62	63	81	86	107	107	115	137	147
Reproductive Isolation Value	0.32	0.54	0.50	0.50	0.82	0.37	0.67	0.53	1.15	0.73	0.82	0.81	0.87	0.87
Distance (continued)	137	150	165	189	219	239	247	53	55	62	105	179	169	
Isolation (continued)	0.50	0.57	0.91	0.93	1.5	1.22	0.82	0.99	0.21	0.56	0.41	0.72	1.15	

Polyploidy

A species may originate from an accident during cell division that results in extra sets of chromosomes, a condition called **polyploidy**. Polyploid speciation occasionally occurs in animals; for example, the gray tree frog *Hyla versicolor* (see Figure 23.16) is thought to have originated in this way. However, polyploidy is far more common in plants. In fact, botanists estimate that more than 80% of the plant species alive today are descended from ancestors that formed by polyploid speciation.

▼ Figure 24.9 Sympatric speciation by autopolyploidy.



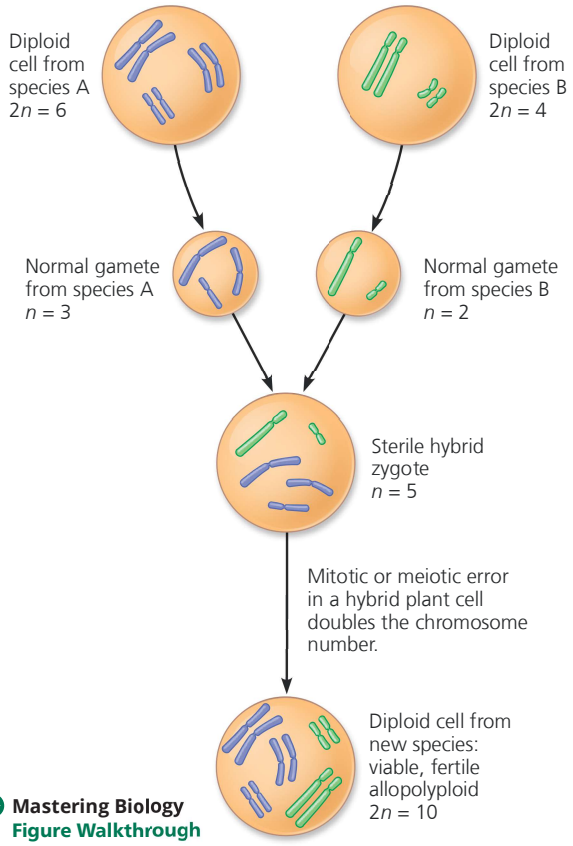
Two distinct forms of polyploidy have been observed in plant (and a few animal) populations. An **autopolyploid** (from the Greek *autos*, self) is an individual that has more than two chromosome sets that are all derived from a single species. In plants, for example, a failure of cell division could double a cell's chromosome number from the original number ($2n$) to a tetraploid number ($4n$) **(Figure 24.9)**.

A tetraploid can produce fertile tetraploid offspring by self-pollinating or by mating with other tetraploids. In addition, the tetraploids are reproductively isolated from $2n$ plants of the original population because the triploid ($3n$) offspring of such unions have reduced fertility. Thus, in just one generation, autopolyploidy can generate reproductive isolation without any geographic separation.

A second form of polyploidy can occur when two different species interbreed and produce hybrid offspring. Most such hybrids are sterile because the set of chromosomes from one species cannot pair during meiosis with the set of chromosomes from the other species. However, an infertile hybrid may be able to propagate itself asexually (as many plants can do). In subsequent generations, various mechanisms can change a sterile hybrid into a fertile polyploid called an **allopolyploid** **(Figure 24.10)**. The allopolyploids are fertile when mating with each other but cannot interbreed with either parent species; thus, they represent a new biological species. The new species has a diploid chromosome number equal to the sum of the diploid chromosome numbers of the two parent species.

Although it can be challenging to study speciation in the field, scientists have documented at least five new plant species that have originated by polyploid speciation since 1850. One of these examples involves the origin of a new species of goatsbeard plant (genus *Tragopogon*) in the Pacific Northwest. *Tragopogon* first arrived in the region when humans introduced

▼ Figure 24.10 One mechanism for allopolyploid speciation in plants. Most hybrids are sterile because their chromosomes are not homologous and cannot pair during meiosis. However, such a hybrid may be able to reproduce asexually. This diagram traces one mechanism by which sterile hybrids can give rise to fertile allopolyploids that are members of a new species.

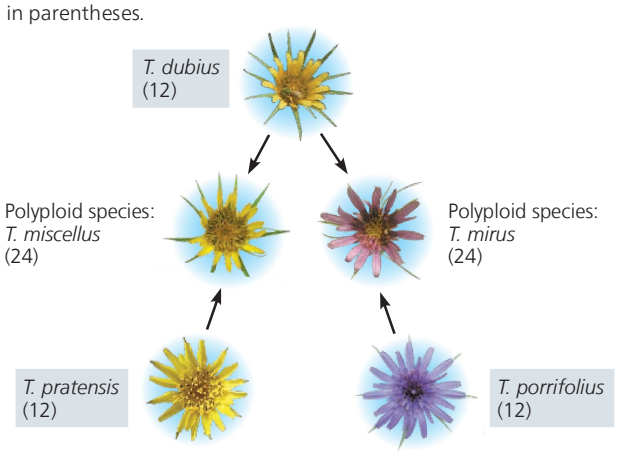


Mastering Biology
Figure Walkthrough

three European species in the early 1900s: *T. pratensis, T. dubius*, and *T. porrifolius*. These three species are now common in the Pacific Northwest and many other parts of North America. In 1950, a new *Tragopogon* species was discovered near the Idaho-Washington border, a region where all three European species also were found. Genetic analyses revealed that this new species, *Tragopogon miscellus*, is an allopolyploid that originated from a hybrid of two of the European species **(Figure 24.11)**. Although the *T. miscellus* population grows mainly by reproduction of its own members, hybridization between the parent species (followed by a mitotic or meiotic error that doubles the chromosome number) continues to add new members to the *T. miscellus* population. Later, scientists discovered another new *Tragopogon* species, *T. mirus*, which also arose by polyploid speciation.

Many important agricultural crops—such as oats, cotton, potatoes, tobacco, and wheat—are polyploids. For example, the wheat used for bread, *Triticum aestivum*, is an allohexaploid (six sets of chromosomes, two sets from each of three different species). The events that eventually led to modern wheat probably began about 8,000 years ago in the Middle

▼ Figure 24.11 Allopolyploid speciation in *Tragopogon*. The gray boxes indicate the parent species of the two new polyploid species. The diploid chromosome number of each species is shown in parentheses.



VISUAL SKILLS *Based on this diagram, identify the two parent species of each polyploid species.*

East when an early cultivated wheat species hybridized with a wild grass. Today, plant geneticists generate new polyploids in the laboratory by using chemicals that induce meiotic and mitotic errors. By harnessing the evolutionary process, researchers can produce new polyploid species with desired qualities, such as a polyploid that combines the high yield of wheat with the hardiness of rye.

Mastering Biology **Animation: Speciation by Changes in Ploidy**

Sexual Selection

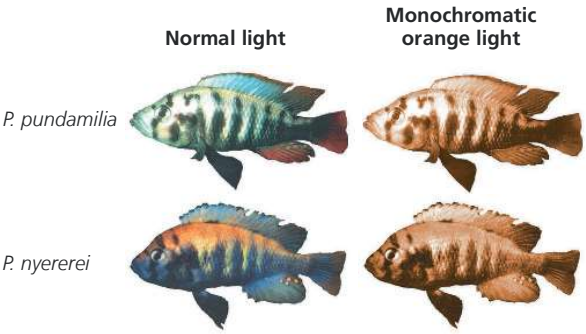
There is evidence that sympatric speciation can also be driven by sexual selection. Clues to how this can occur have been found in cichlid fish from one of Earth's hot spots of animal speciation, East Africa's Lake Victoria. This lake was once home to as many as 600 species of cichlids. Genetic data indicate that these species originated within the last 100,000 years from a small number of colonizing species that arrived from other lakes and rivers. How did so many species—more than double the number of freshwater fish species known in all of Europe—originate within a single lake?

One hypothesis is that subgroups of the original cichlid populations adapted to different food sources and the resulting genetic divergence contributed to speciation in Lake Victoria. But sexual selection, in which (typically) females select males based on their appearance (see Concept 23.4), may also have been a factor. Researchers have studied two closely related sympatric species of cichlids that differ mainly in the coloration of breeding males: Breeding *Pundamilia pundamilia* males have a blue-tinged back, whereas breeding *Pundamilia nyererei* males have a red-tinged back **(Figure 24.12)**. Their results suggest that mate choice based on male breeding coloration can act as a reproductive barrier that keeps the gene pools of these two species separate.

▼ Figure 24.12 Inquiry

Does sexual selection in cichlids result in reproductive isolation?

Experiment Researchers placed males and females of *Pundamilia pundamilia* and *P. nyererei* together in two aquarium tanks, one with natural light and one with a monochromatic orange lamp. Under normal light, the two species are noticeably different in male breeding coloration; under monochromatic orange light, the two species are very similar in color. The researchers then observed the mate choices of the females in each tank.



Results Under normal light, females of each species strongly preferred males of their own species. But under orange light, females of each species responded indiscriminately to males of both species. The resulting hybrids were viable and fertile.

Conclusion The researchers concluded that mate choice by females based on male breeding coloration can act as a reproductive barrier that keeps the gene pools of these two species separate. Since the species can still interbreed when this prezygotic barrier is breached in the laboratory, the genetic divergence between the species is likely to be small. This suggests that speciation in nature has occurred relatively recently.

Data from O. Seehausen and J. J. M. van Alphen, The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex), *Behavioral Ecology and Sociobiology* 42:1–8 (1998).

WHAT IF? *Suppose that female cichlids living in the murky waters of a polluted lake could not distinguish colors well. In such waters, how might the gene pools of these species change over time?*

Habitat Differentiation

Sympatric speciation can also occur when a subpopulation exploits a habitat or resource not used by the parent population. Consider the North American apple maggot fly (*Rhagoletis pomonella*), a pest of apples. The fly's original habitat was the native hawthorn tree (see Figure 24.3a), but about 200 years ago, some populations colonized apple trees that had been introduced by European settlers. Apple maggot flies usually mate on or near their host plant. This results in a prezygotic barrier (habitat isolation) between populations that feed on apples and populations that feed on hawthorns. Furthermore, because apples mature more quickly than hawthorn fruit, natural selection has favored apple-feeding flies with rapid development. These apple-feeding populations now show temporal isolation from the hawthorn-feeding

R. pomonella, providing a second prezygotic barrier to gene flow between the two populations. Researchers also have identified alleles that benefit the flies that use one host plant but harm the flies that use the other host plant. Natural selection operating on these alleles has provided a postzygotic barrier to reproduction, further limiting gene flow. Altogether, although the two populations are still classified as subspecies rather than separate species, sympatric speciation appears to be well under way.

Allopatric and Sympatric Speciation: *A Review*

Now let's recap the processes by which new species form. In allopatric speciation, a new species forms in geographic isolation from its parent population. Geographic isolation severely restricts gene flow. Intrinsic barriers to reproduction with members of the parent population may then arise as a by-product of genetic changes that occur within the isolated population. Many different processes can produce such genetic changes, including natural selection under different environmental conditions, genetic drift, and sexual selection. Once formed, reproductive barriers that arise in allopatric populations can prevent interbreeding with the parent population even if the populations come back into contact.

Sympatric speciation, in contrast, requires the emergence of a reproductive barrier that isolates a subset of a population from the remainder of the population in the same area. Though rarer than allopatric speciation, sympatric speciation can occur when gene flow to and from the isolated subpopulation is blocked. This can occur as a result of polyploidy, a condition in which an organism has extra sets of chromosomes. Sympatric speciation also can result from sexual selection. Finally, sympatric speciation can occur when a subset of a population becomes reproductively isolated because of natural selection that results from a switch to a habitat or food source not used by the parent population.

Having reviewed the geographic context in which species originate, we'll next explore in more detail what can happen when new or partially formed species come into contact.

Mastering Biology **HHMI Video: Anole Lizards: An Example of Speciation**

hhmi BioInteractive

CONCEPT CHECK 24.2

1. Summarize key differences between allopatric and sympatric speciation. Which type of speciation is more common, and why?
2. Describe two mechanisms that can decrease gene flow in sympatric populations, thereby making sympatric speciation more likely to occur.
3. **WHAT IF?** Is allopatric speciation more likely to occur on an island close to a mainland or on a more isolated island of the same size? Explain your prediction.
4. **MAKE CONNECTIONS** Review the process of meiosis in Figure 13.8. Describe how an error during meiosis could lead to polyploidy.

For suggested answers, see Appendix A.

CONCEPT 24.3

Hybrid zones reveal factors that cause reproductive isolation

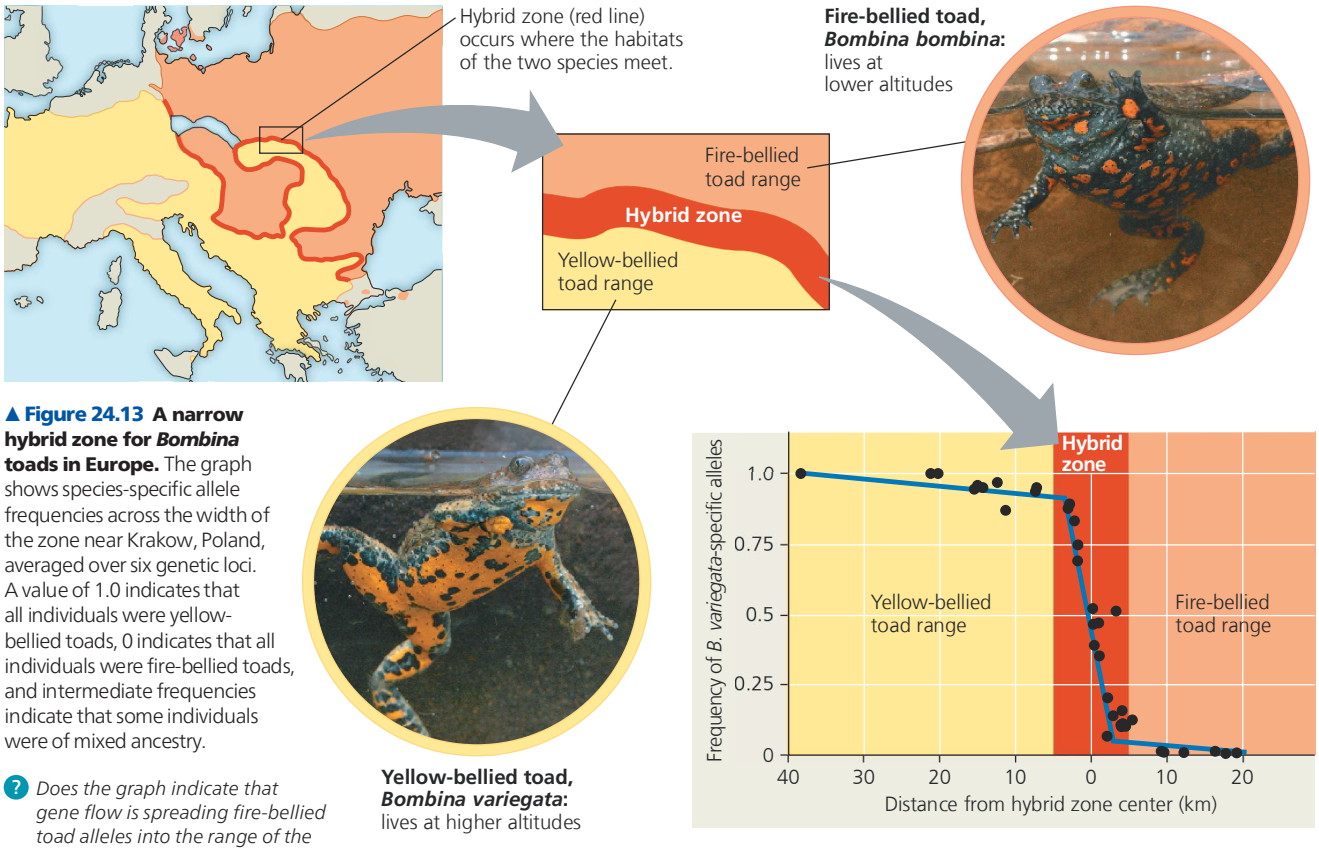
What happens if species with incomplete reproductive barriers come into contact with one another? One possible outcome is the formation of a **hybrid zone**, a region in which members of different species meet and mate, producing at least some offspring of mixed ancestry. In this section, we'll explore hybrid zones and what they reveal about factors that cause the evolution of reproductive isolation.

Patterns Within Hybrid Zones

Some hybrid zones form as narrow bands, such as the one depicted in **Figure 24.13** for the yellow-bellied toad (*Bombina variegata*) and its close relative, the fire-bellied toad (*B. bombina*). This hybrid zone, represented by the red line on the map, extends for 4,000 km but is less than 10 km wide in most places. The hybrid zone occurs where the higher-altitude habitat of the yellow-bellied toad meets the lowland habitat of the fire-bellied toad. Across a given "slice" of the zone, the frequency of alleles specific to yellow-bellied toads typically decreases from close to 100% at the edge where only yellow-bellied toads are found to around 50% in the central portion of the zone and to close to 0% at the edge where only fire-bellied toads are found.

What causes such a pattern of allele frequencies across a hybrid zone? We can infer that there is an obstacle to gene flow—otherwise, alleles from one parent species would also be common in the gene pool of the other parent species. Are geographic barriers reducing gene flow? Not in this case, since the toads can move throughout the hybrid zone. A more important factor is that hybrid toads have increased rates of embryonic mortality and a variety of morphological abnormalities, including ribs that are fused to the spine and malformed tadpole mouthparts. Because the hybrids have poor survival and reproduction, they produce few viable offspring with members of the parent species. As a result, hybrid individuals rarely serve as a stepping-stone from which alleles are passed from one species to the other. Outside the hybrid zone, additional obstacles to gene flow may be provided by natural selection in the different environments in which the parent species live.

Hybrid zones typically are located wherever the habitats of the interbreeding species meet. Those regions often resemble a group of isolated patches scattered across the landscape—more like the pattern of spots on a Dalmatian than the continuous band shown in Figure 24.13. But regardless of whether they have complex or simple spatial patterns, hybrid zones form when two species lacking complete barriers to reproduction come into contact. What happens when the habitats of the interbreeding species change over time?



▲ Figure 24.13 A narrow hybrid zone for *Bombina* toads in Europe. The graph shows species-specific allele frequencies across the width of the zone near Krakow, Poland, averaged over six genetic loci. A value of 1.0 indicates that all individuals were yellow-bellied toads, 0 indicates that all individuals were fire-bellied toads, and intermediate frequencies indicate that some individuals were of mixed ancestry.

? *Does the graph indicate that gene flow is spreading fire-bellied toad alleles into the range of the yellow-bellied toad? Explain.*

Hybrid Zones and Environmental Change

A change in environmental conditions can alter where the habitats of interbreeding species meet. When this happens, an existing hybrid zone can move to a new location, or a novel hybrid zone may form.

For example, black-capped chickadees (*Poecile atricapillus*) and Carolina chickadees (*P. carolinensis*) interbreed in a narrow hybrid zone that runs from New Jersey to Kansas. Recent studies have shown that the location of this hybrid zone has shifted northward as the climate has warmed **(Figure 24.14)**. In another example, a series of warm winters prior to 2003 enabled the southern flying squirrel (*Glaucomys volans*) to expand northward into the range of the northern flying squirrel, *G. sabrinus*. Previously, the ranges of these two species had not overlapped. Genetic analyses showed that these flying squirrels began to hybridize where their ranges came into contact, thereby forming a novel hybrid zone induced by climate change.

Finally, note that a hybrid zone can be a source of novel genetic variation that improves the ability of one or both parent species to cope with changing environmental conditions. This can occur when an allele found only in one parent species is transferred first to hybrid individuals and then to the other parent species when hybrids breed with the second parent species. Recent genetic analyses have shown that hybridization has been a source for such novel genetic variation in some insect, mammal, bird, and plant species. In the **Problem-Solving Exercise**, you can examine one such example: a case in which hybridization may have led to the transfer of insecticide-resistance alleles between species of mosquitoes that transmit malaria.

▼ Figure 24.14 A shift in a hybrid zone resulting from climate change. Black-capped **(a)** and Carolina chickadees **(b)** interbreed in a hybrid zone that runs from Kansas to New Jersey. In Pennsylvania, the center of this hybrid zone moved 12 km to the north from 2002 to 2012. This shift is consistent with predictions based on the warmer winter temperatures that have resulted from climate change.



(a) Black-capped chickadee (*Poecile atricapillus*)



(b) Carolina chickadee (*Poecile carolinensis*)

PROBLEM-SOLVING EXERCISE

Is hybridization promoting insecticide resistance in mosquitoes that transmit malaria?

Malaria is a leading cause of human illness and mortality worldwide, with 200 million people infected and 600,000 deaths each year. In the 1960s, the incidence of malaria was reduced, owing to the use of insecticides that killed mosquitoes in the genus *Anopheles*, which transmit the disease from person to person. But today, mosquitoes are becoming resistant to insecticides—causing a resurgence in malaria.



Insecticide-treated bed nets have helped reduce cases of malaria in many countries, but resistance to insecticides is rising in mosquito populations.

Instructors: A version of this Problem-Solving Exercise can be assigned in **Mastering Biology**.

In this exercise, you will investigate whether alleles encoding resistance to insecticides have been transferred between closely related species of *Anopheles*.

Your Approach The principle guiding your investigation is that DNA analyses can detect the transfer of resistance alleles between closely related mosquito species. To find out whether such transfers have occurred, you will analyze DNA results from two species of mosquitoes that transmit malaria (*Anopheles gambiae* and *A. coluzzii*) and from *A. gambiae* × *A. coluzzii* hybrids.

Your Data Resistance to DDT and other insecticides in *Anopheles* is affected by a sodium channel gene, *kdr*. The *r* allele of this gene confers resistance, while the wild-type (+/+) genotype is not resistant. Researchers sequenced the *kdr* gene from mosquitoes collected in Mali during three time periods: pre-2006 (2002 and 2004), 2006, and post-2006 (2009–2012). *A. gambiae* and *A. coluzzii* were collected during all three time periods, but their hybrids only occurred in 2006, the first year that insecticide-treated bed nets were used to reduce the spread of malaria. A likely explanation is that the introduction of the treated bed nets may have briefly favored hybrid individuals, which are usually at a selective disadvantage.

Observed numbers of mosquitoes by *kdr* genotype

	+/+	+/*r*	*r*/*r*
***A. gambiae*:**			
Pre-2006	3	5	2
2006	8	8	7
Post-2006	3	3	57
***Hybrids*: 2006**	10	7	0
***A. coluzzii*:**			
Pre-2006	226	0	0
2006	70	7	0
Post-2006	79	127	94

Your Analysis

1. **(a)** Calculate the *kdr* genotype frequencies in *A. gambiae* for each time period. To do this, divide the number of individuals that have a given genotype by the total number of individuals observed for that time period. **(b)** How did the *kdr* genotype frequencies change over time? Describe a hypothesis that accounts for these observations.
2. How did the frequencies of *kdr* genotypes change over time in *A. coluzzii*? Describe a hypothesis that accounts for these observations.
3. Do these results indicate that hybridization can lead to the transfer of adaptive alleles? Explain.
4. Predict how the transfer of the *r* allele to *A. coluzzii* populations could affect the number of malaria cases in the years immediately following the transfer.

Hybrid Zones over Time

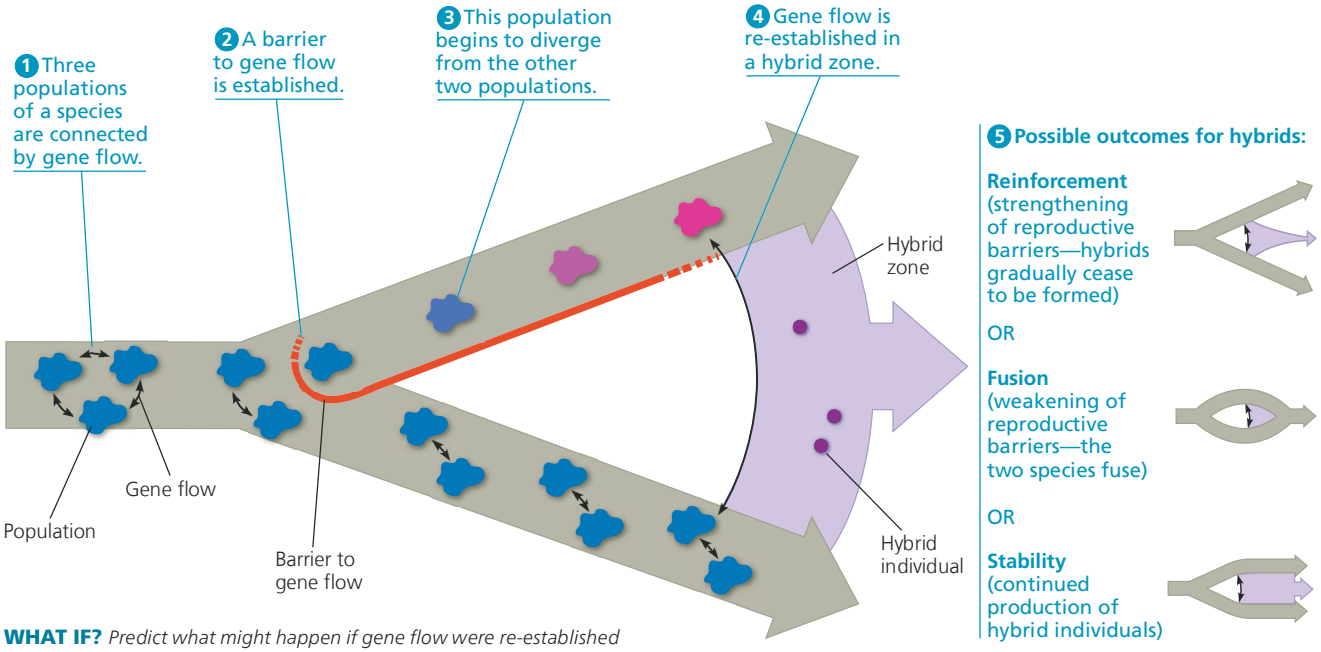
Studying a hybrid zone is like observing a naturally occurring experiment on speciation. Will the hybrids become reproductively isolated from their parents and form a new species? This has occurred by polyploid speciation in some cases, as we saw for the formation of two new species of goatsbeard plants (see Figure 24.11). Hybridization also has led to what may turn out to be a new species of finch in the Galápagos archipelago: A 2018 study found that descendants of hybrids between the large cactus finch (*Geospiza conirostris*) and the medium ground finch (*G. fortis*) are becoming reproductively isolated from both parent species. As of 2019, this emerging species is known informally as "Big Bird."

In other cases, however, interspecific hybrids do not become reproductively isolated from their parent species. In such situations, there are three common outcomes for a hybrid zone over time: reinforcement of barriers, fusion of species, or stability **(Figure 24.15)**. Let's examine what studies suggest about these possibilities.

Reinforcement: Strengthening Reproductive Barriers

Hybrids often are less fit than members of their parent species. In such cases, natural selection should strengthen prezygotic barriers to reproduction, reducing the formation of unfit hybrids. Because this process involves *reinforcing* reproductive barriers, it is called **reinforcement**. If reinforcement is occurring, a logical prediction is that barriers to reproduction between species should be stronger for sympatric populations than for allopatric populations.

▼ Figure 24.15 Formation of a hybrid zone and common outcomes for hybrids over time.
The thick gray and purple arrows represent the passage of time.



WHAT IF? *Predict what might happen if gene flow were re-established at step 3 in this process.*

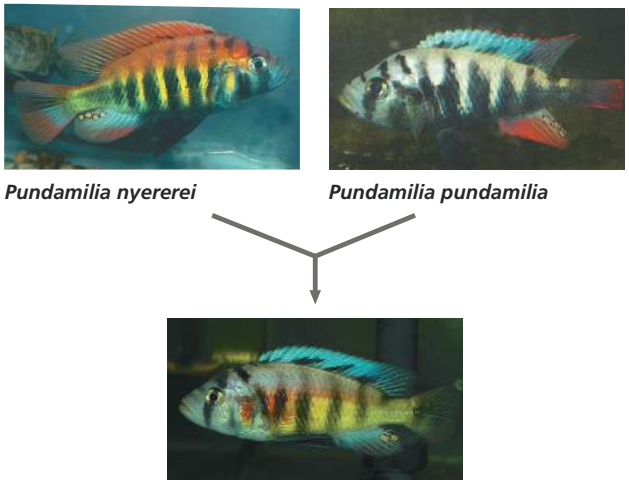
As an example, let's consider two species of European flycatcher, the pied flycatcher (*Ficedula hypoleuca*) and the collared flycatcher (*Ficedula albicollis*). In allopatric populations of these birds, males of the two species closely resemble one another, while in sympatric populations, the males look very different. Female flycatchers do not select males of the other species when given a choice between males from sympatric populations, but they frequently do make mistakes when selecting between males from allopatric populations. Thus, barriers to reproduction are stronger in birds from sympatric populations than in birds from allopatric populations, as you would predict if reinforcement were occurring. Similar results have been observed in a number of organisms, including some fishes, insects, plants, and other birds.

Fusion: Weakening Reproductive Barriers

Barriers to reproduction may be weak when two species meet in a hybrid zone. Indeed, so much gene flow may occur that reproductive barriers weaken further and the gene pools of the two species become increasingly alike. In effect, the speciation process reverses, eventually causing the two hybridizing species to fuse into a single species.

For example, genetic and morphological evidence indicates that the recent loss of the large tree finch from the Galápagos island of Floreana resulted from extensive hybridization with another finch species on that island. Such a situation also may be occurring among Lake Victoria cichlids **(Figure 24.16)**. Many pairs of ecologically similar cichlid species are reproductively isolated because the females of one species prefer to mate with males of one color, while females of the other species prefer to mate with males of a different color (see Figure 24.12). Results from field and laboratory studies indicate that murky waters caused by

▼ Figure 24.16 Fusion: the breakdown of reproductive barriers.
Increasingly cloudy water in Lake Victoria over the past several decades may have weakened reproductive barriers between *P. nyererei* and *P. pundamilia*. In areas of cloudy water, the two species have hybridized extensively, causing their gene pools to fuse.



Pundamilia nyererei ***Pundamilia pundamilia***

Pundamilia "turbid water," hybrid offspring from a location with turbid water

pollution have reduced the ability of females to use color to distinguish males of their own species from males of closely related species. In some polluted waters, many hybrids have been produced, leading to fusion of the parent species' gene pools and a loss of species.

Stability: Continued Formation of Hybrid Individuals

Many hybrid zones are stable in the sense that hybrids continue to be produced. In some cases, this occurs because the hybrids survive or reproduce better than members of either parent species, at least in certain habitats or years. But stable hybrid zones have also been observed in cases where the hybrids are selected *against*—an unexpected result.

For example, hybrids continue to form in the *Bombina* hybrid zone even though they are strongly selected against. One explanation relates to the narrowness of the *Bombina* hybrid zone (see Figure 24.13). Evidence suggests that members of both parent species migrate into the zone from the parent populations located outside the zone, thus leading to the continued production of hybrids. If the hybrid zone were wider, this would be less likely to occur, since the center of the zone would receive little gene flow from distant parent populations located outside the hybrid zone.

Sometimes the outcomes in hybrid zones match our predictions (European flycatchers and cichlid fishes), and sometimes they don't (*Bombina*). But whether our predictions are upheld or not, events in hybrid zones can shed light on how barriers to reproduction between closely related species change over time. In the next section, we'll examine how interactions between hybridizing species can also provide a glimpse into the speed and genetic control of speciation.

CONCEPT CHECK 24.3

1. What are hybrid zones, and why can they be viewed as "natural laboratories" in which to study speciation?
2. **WHAT IF?** Consider two species that diverged while geographically separated but resumed contact before reproductive isolation was complete. Predict the outcome over time if the two species mated indiscriminately and (a) hybrid offspring survived and reproduced more poorly than offspring from intraspecific matings or (b) hybrid offspring survived and reproduced as well as offspring from intraspecific matings.

For suggested answers, see Appendix A.

CONCEPT 24.4

Speciation can occur rapidly or slowly and can result from changes in few or many genes

Darwin faced many questions when he began to ponder that "mystery of mysteries"—speciation. He found answers to some of those questions when he realized that evolution by natural selection helps explain both the diversity of life and the adaptations of organisms (see Concept 22.2). But biologists since Darwin have continued to ask fundamental questions about speciation. How long does it take for new species to form? And how many genes change when one species splits into two? Answers to these questions are also emerging.

The Time Course of Speciation

We can gather information about how long it takes new species to form from broad patterns in the fossil record and from studies that use morphological data (including fossils) or molecular data to assess the time interval between speciation events in particular groups of organisms.

Patterns in the Fossil Record

The fossil record includes many episodes in which new species appear suddenly in a geologic stratum, persist essentially unchanged through several strata, and then disappear. For example, there are dozens of species of marine invertebrates that make their debut in the fossil record with novel morphologies, but then change little for millions of years before becoming extinct. The term **punctuated equilibria** is used to describe these periods of apparent stasis punctuated by sudden change **(Figure 24.17a)**. Other species do not show a punctuated pattern; instead, they appear to have changed more gradually over long periods of time **(Figure 24.17b)**.

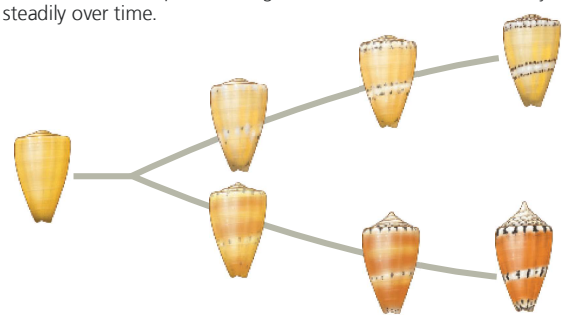
What might punctuated and gradual patterns tell us about how long it takes new species to form? Suppose that a species survived for 5 million years, but most of the morphological changes that caused it to be designated a new species occurred during its first 50,000 years—just 1% of the total existence of

▼ Figure 24.17 Two models for the tempo of speciation.

(a) Punctuated model. New species change most as they branch from a parent species and then change little for the rest of their existence.



(b) Gradual model. Species diverge from one another more slowly and steadily over time.



the species. Time periods this short (in geologic terms) often cannot be distinguished in fossil strata, in part because the rate of sediment accumulation may be too slow to separate layers this close in time. Thus, based on its fossils, the species would seem to have appeared suddenly and then lingered with little or no change before becoming extinct. Even though such a species may have originated more slowly than its fossils suggest (in this case taking up to 50,000 years), a punctuated pattern indicates that speciation occurred relatively rapidly. For species whose fossils changed much more gradually, we also cannot tell exactly when a new biological species formed, since information about reproductive isolation does not fossilize. However, it is likely that speciation in such groups occurred relatively slowly, perhaps taking millions of years.

Mastering Biology
Interview with Stephen Jay Gould: An "architect" of the concept of punctuated equilibria



Speciation Rates

The existence of fossils that display a punctuated pattern suggests that once the process of speciation begins, it can be completed relatively rapidly—a suggestion supported by many studies. For example, rapid speciation appears to have produced the wild sunflower *Helianthus anomalus*. Genetic evidence indicates that this species originated by the hybridization of two other sunflower species, *H. annuus* and *H. petiolaris*. The hybrid species *H. anomalus* is ecologically distinct and reproductively isolated from both parent species **(Figure 24.18)**. Unlike the outcome of allopolyploid speciation, in which there is a change in chromosome number after hybridization, in these sunflowers the two parent species and the hybrid all have the same number of chromosomes ($2n = 34$). How, then, did speciation occur? To study this question, researchers performed an experiment designed to mimic events in nature **(Figure 24.19)**. Their results indicated that natural selection could produce extensive genetic changes in hybrid populations over short periods of time. These changes appear to have caused the hybrids to diverge reproductively from their parents and form a new species, *H. anomalus*.

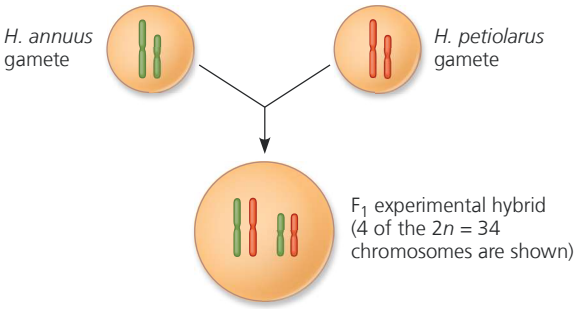
▼ Figure 24.18 A hybrid sunflower species and its dry sand dune habitat. The wild sunflower *Helianthus anomalus* shown here originated via the hybridization of two other sunflowers, *H. annuus* and *H. petiolaris*, which live in nearby but moister environments.



▼ Figure 24.19 Inquiry

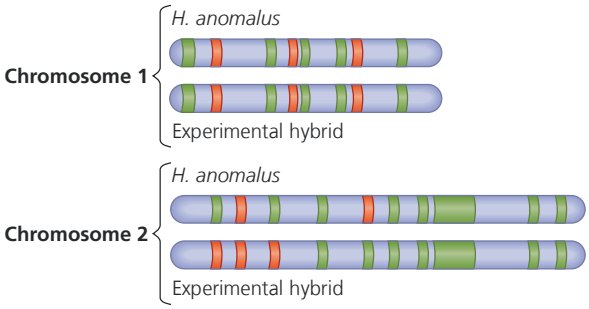
How does hybridization lead to speciation in sunflowers?

Experiment Loren Rieseberg and his colleagues crossed the two parent sunflower species, *H. annuus* and *H. petiolaris*, to produce experimental hybrids in the laboratory (for each gamete, only two of the $n = 17$ chromosomes are shown).



Note that in the first (F_1) generation, each chromosome of the experimental hybrids consisted entirely of DNA from one or the other parent species. The researchers then tested whether the F_1 and subsequent generations of experimental hybrids were fertile. They also used species-specific genetic markers to compare the chromosomes in the experimental hybrids with the chromosomes in the naturally occurring hybrid *H. anomalus*.

Results Although only 5% of the F_1 experimental hybrids were fertile, after just four more generations the hybrid fertility rose to more than 90%. The chromosomes of individuals from this fifth hybrid generation differed from those in the F_1 generation (see above) but were similar to those in *H. anomalus* individuals from natural populations:



Conclusion Over time, the chromosomes in the population of experimental hybrids became similar to the chromosomes of *H. anomalus* individuals from natural populations. This suggests that the observed rise in the fertility of the experimental hybrids may have occurred as selection eliminated regions of DNA from the parent species that were not compatible with one another. Overall, it appeared that the initial steps of the speciation process occurred rapidly and could be mimicked in a laboratory experiment.

Data from L. H. Rieseberg et al., Role of gene interactions in hybrid speciation: evidence from ancient and experimental hybrids, *Science* 272:741–745 (1996).

WHAT IF? *The increased fertility of the experimental hybrids could have resulted from natural selection for thriving under laboratory conditions. Evaluate this alternative explanation for the result.*

The sunflower example, along with the apple maggot fly, Lake Victoria cichlid, and fruit fly examples discussed earlier, suggests that new species can arise rapidly *once divergence begins*. But what is the total length of time between speciation events? This interval consists of the time that elapses before populations of a newly formed species start to diverge from one another plus the time it takes for speciation to be complete once divergence begins. It turns out that the total time between speciation events varies considerably. In a survey of data from 84 groups of plants and animals, speciation intervals ranged from 4,000 years (in cichlids of Lake Nabugabo, Uganda) to 40 million years (in some beetles). Overall, the time between speciation events averaged 6.5 million years and was rarely less than 500,000 years.

These data suggest that on average, millions of years may pass before a newly formed plant or animal species will itself give rise to another new species. As you'll read in Concept 25.4, this finding has implications for how long it takes life on Earth to recover from mass extinction events. Moreover, the extreme variability in the time it takes new species to form indicates that organisms do not have an internal "speciation clock" that causes them to produce new species at regular intervals. Instead, speciation begins only after gene flow between populations is interrupted, perhaps by changing environmental conditions or by unpredictable events, such as a storm that transports a few individuals to a new area. Furthermore, once gene flow is interrupted, the populations must diverge genetically to such an extent that they become reproductively isolated—all before other events cause gene flow to resume, possibly reversing the speciation process (see Figure 24.16).

Studying the Genetics of Speciation

Studies of ongoing speciation (as in hybrid zones) can reveal traits that cause reproductive isolation. By identifying the genes that control those traits, scientists can explore a fundamental question of evolutionary biology: How many genes influence the formation of new species?

In some cases, the evolution of reproductive isolation results from the effects of a single gene. For example, in Japanese snails of the genus *Euhadra*, a change in a single gene results in a mechanical barrier to reproduction. This gene controls the direction in which the shells spiral. When their shells spiral in different directions, the snails' genitalia are oriented in a manner that prevents mating (Figure 24.3f and g show a similar example). Recent genetic analyses have uncovered other single genes that cause reproductive isolation in fruit flies or mice.

A major barrier to reproduction between two closely related species of monkey flower, *Mimulus cardinalis* and *M. lewisii*, also appears to be influenced by a relatively small number of genes. These two species are isolated by several prezygotic and postzygotic barriers. Of these, one prezygotic barrier, pollinator choice, accounts for most of the isolation: In a hybrid zone between *M. cardinalis* and *M. lewisii*, nearly 98% of pollinator visits were restricted to one species or the other.

▼ Figure 24.20 A locus that influences pollinator choice. Pollinator preferences provide a strong barrier to reproduction between *Mimulus lewisii* and *M. cardinalis*. After transferring the *M. lewisii* allele for a flower-color locus into *M. cardinalis* and vice versa, researchers observed a shift in some pollinators' preferences.



(a) Typical *Mimulus lewisii*



(b) *M. lewisii* with an *M. cardinalis* flower-color allele



(c) Typical *Mimulus cardinalis*



(d) *M. cardinalis* with an *M. lewisii* flower-color allele

WHAT IF? *If* M. cardinalis *individuals that had the* M. lewisii yup *allele were planted in an area that housed both monkey flower species, how might the production of hybrid offspring be affected?*

The two monkey flower species are visited by different pollinators: Hummingbirds prefer the red-flowered *M. cardinalis*, and bumblebees prefer the pink-flowered *M. lewisii*. Pollinator choice is affected by at least two loci in the monkey flowers, one of which, the "yellow upper," or *yup*, locus, influences flower color **(Figure 24.20)**. By crossing the two parent species to produce F_1 hybrids and then performing repeated backcrosses of these F_1 hybrids to each parent species, researchers succeeded in transferring the *M. cardinalis* allele at this locus into *M. lewisii*, and vice versa. In a field experiment, *M. lewisii* plants with the *M. cardinalis yup* allele received 68-fold more visits from hummingbirds than did wild-type *M. lewisii*. Similarly, *M. cardinalis* plants with the *M. lewisii yup* allele received 74-fold more visits from bumblebees than did wild-type *M. cardinalis*. Thus, a mutation at a single locus can influence pollinator preference and hence contribute to reproductive isolation in monkey flowers.

In other organisms, the speciation process is influenced by larger numbers of genes and gene interactions. For example, hybrid sterility between two subspecies of the fruit fly *Drosophila pseudoobscura* results from gene interactions among at least four loci, and postzygotic isolation in the sunflower hybrid zone

discussed earlier is influenced by at least 26 chromosome segments (and an unknown number of genes). Overall, studies suggest that few or many genes can influence the evolution of reproductive isolation and hence the emergence of a new species.

From Speciation to Macroevolution

As you've seen, speciation may begin with differences as small as the color on a cichlid's back. However, as speciation occurs again and again, such differences can accumulate and become more pronounced, eventually leading to the formation of new groups of organisms that differ greatly from their ancestors (as in the origin of whales from terrestrial mammals; see Figure 22.20). Moreover, as one group of organisms increases in size by producing many new species, another group of organisms may shrink, losing species to extinction. The cumulative effects of many such speciation and extinction events have helped shape the sweeping evolutionary changes that are documented in the fossil record. In the next chapter, we turn to such large-scale evolutionary changes as we begin our study of macroevolution.

CONCEPT CHECK 24.4

1. Speciation can occur rapidly between diverging populations, yet the time between speciation events is often more than a million years. Explain this apparent contradiction.
2. Summarize evidence that the *yup* locus acts as a prezygotic barrier to reproduction in two species of monkey flowers. Do these results show that the *yup* locus alone controls barriers to reproduction between these species? Explain.
3. **MAKE CONNECTIONS** Compare Figures 13.12 and 24.19. What cellular process could cause the hybrid chromosomes in Figure 24.19 to have DNA from both parent species? Explain.

For suggested answers, see Appendix A.

24 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

CONCEPT 24.1

The biological species concept emphasizes reproductive isolation *(pp. 507–510)*

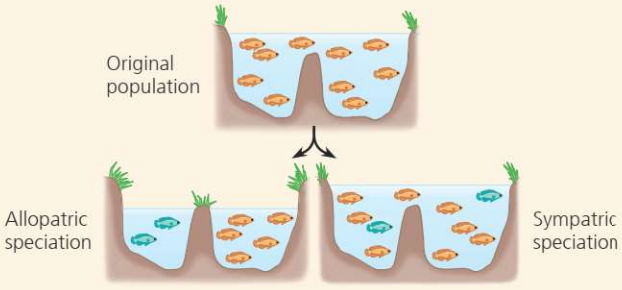
- A biological **species** is a group of populations whose individuals may interbreed and produce viable, fertile offspring with each other but not with members of other species.
- New species form when **reproductive isolation** between populations develops through the establishment of **prezygotic** or **postzygotic barriers** that separate gene pools.

? *Explain the role of gene flow in the biological species concept.*

CONCEPT 24.2

Speciation can take place with or without geographic separation *(pp. 511–516)*

- In **allopatric speciation**, gene flow is reduced when two populations of one species become geographically separated from each other. One or both populations may undergo evolutionary change during the period of separation, resulting in the establishment of barriers to reproduction.



- In **sympatric speciation**, a new species originates while remaining in the same geographic area as the parent species. Plant species (and, more rarely, animal species) have evolved sympatrically through **polyploidy**. Sympatric speciation can also result from sexual selection and habitat shifts.

? *Can factors that cause sympatric speciation also cause allopatric speciation? Explain.*

CONCEPT 24.3

Hybrid zones reveal factors that cause reproductive isolation *(pp. 516–520)*

- Many groups of organisms form **hybrid zones** in which members of different species meet and mate, producing at least some offspring of mixed ancestry.
- Many hybrid zones are *stable*, in that hybrid offspring continue to be produced over time. In others, **reinforcement** strengthens prezygotic barriers to reproduction, thus decreasing the formation of unfit hybrids. In still other hybrid zones, barriers to reproduction may weaken over time, resulting in the *fusion* of the species' gene pools (reversing the speciation process).

? *What factors can support the long-term stability of a hybrid zone if the parent species live in different environments?*

CONCEPT 24.4

Speciation can occur rapidly or slowly and can result from changes in few or many genes *(pp. 520–523)*

- New species can form rapidly once divergence begins, but it can take millions of years for that to happen. The time interval between speciation events varies considerably, from a few thousand years to tens of millions of years.
- Researchers have identified particular genes involved in some cases of speciation. Speciation can be driven by a few or many genes.

? *Is speciation something that happened only in the distant past, or are new species continuing to arise today? Explain.*

TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

1. The *largest* unit within which gene flow can readily occur is a
(A) population. (C) genus.
(B) species. (D) hybrid.

2. Males of different species of the fruit fly *Drosophila* that live in the same parts of the Hawaiian Islands have different elaborate courtship rituals. These rituals involve fighting other males and making stylized movements that attract females. What type of reproductive isolation does this represent?
(A) habitat isolation (C) behavioral isolation
(B) temporal isolation (D) gametic isolation

3. According to the punctuated equilibria model,
(A) given enough time, most existing species will branch gradually into new species.
(B) most new species accumulate their unique features relatively rapidly as they come into existence, then change little for the rest of their duration as a species.
(C) most evolution occurs in sympatric populations.
(D) speciation is usually due to a single mutation.

Levels 3-4: Applying/Analyzing

4. Bird guides once listed the myrtle warbler and Audubon's warbler as distinct species. Recently, these birds have been classified as eastern and western forms of a single species, the yellow-rumped warbler. Which of the following pieces of evidence, if true, would be cause for this reclassification?
(A) The two forms interbreed often in nature, and their offspring survive and reproduce well.
(B) The two forms live in similar habitats and have similar food requirements.
(C) The two forms have many genes in common.
(D) The two forms are very similar in appearance.

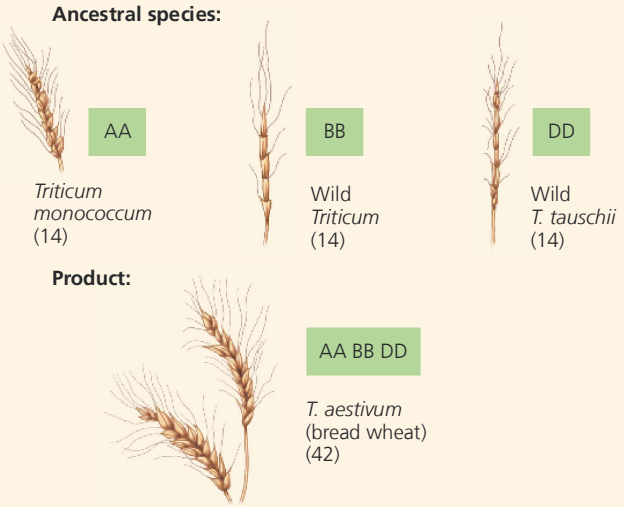
5. Which of the following factors would be the most likely to contribute to allopatric speciation?
(A) The separated population is large, and genetic drift occurs.
(B) Selection pressures in the isolated population are similar to those in the ancestral population.
(C) Gene flow between the two populations is extensive.
(D) Different mutations begin to distinguish the gene pools of the separated populations.

6. Plant species A has a diploid chromosome number of 12. Plant species B has a diploid number of 16. A new species, C, arises as an allopolyploid from A and B. The diploid number for species C would probably be
(A) 14. (C) 28.
(B) 16. (D) 56.

Levels 5-6: Evaluating/Creating

7. **EVOLUTION CONNECTION** Explain the biological basis for assigning all human populations to a single species. Can you think of a scenario by which a second human species could originate in the future?

8. **SCIENTIFIC INQUIRY • DRAW IT** In this chapter, you read that bread wheat (*Triticum aestivum*) is an allohexaploid, containing two sets of chromosomes from each of three different parent species. Genetic analysis suggests that each of the three species pictured following this question contributed chromosome sets to *T. aestivum*. (The capital letters represent sets of chromosomes, each of which can be traced to a particular species, *not* individual genes. The numbers in parentheses are the species' chromosome numbers.) Evidence also indicates that the first polyploidy event began with the spontaneous hybridization of the early cultivated wheat species *T. monococcum* and a wild *Triticum* grass species. Draw a diagram of one possible chain of events that could have produced the allohexaploid *T. aestivum*.



9. **WRITE ABOUT A THEME: INFORMATION** In sexually reproducing species, each individual inherits DNA from both parent organisms. In a short essay (100–150 words), apply this idea to what occurs when organisms of two species that have homologous chromosomes mate and produce (F_1) hybrid offspring. What percentage of the DNA in the F_1 hybrids' chromosomes comes from each parent species? As the hybrids mate and produce F_2 and later-generation hybrid offspring, describe how recombination and natural selection may affect whether the DNA in hybrid chromosomes is derived from one parent species or the other.

10. **SYNTHESIZE YOUR KNOWLEDGE**



Suppose that females of one population of strawberry poison dart frogs (*Dendrobates pumilio*) prefer to mate with males that are orange-red in color. In a different population, females prefer males with yellow skin. Explain how such differences could arise and how they could affect the evolution of reproductive isolation in allopatric versus sympatric populations.

For selected answers, see Appendix A.

25 The History of Life on Earth

KEY CONCEPTS

25.1 Conditions on early Earth made the origin of life possible *p. 526*

25.2 The fossil record documents the history of life *p. 528*

25.3 Key events in life's history include the origins of unicellular and multicellular organisms and the colonization of land *p. 532*

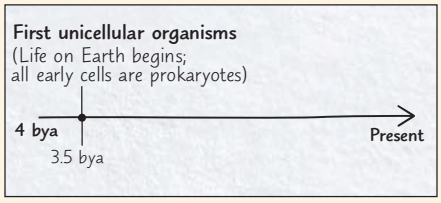
25.4 The rise and fall of groups of organisms reflect differences in speciation and extinction rates *p. 537*

25.5 Major changes in body form can result from changes in the sequences and regulation of developmental genes *p. 544*

25.6 Evolution is not goal oriented *p. 547*

Study Tip

Draw a time line: Draw a time line like the example shown here, and mark when the following key evolutionary events occurred: "oxygen revolution," origin of eukaryotes, first multicellular organisms, colonization of land by large eukaryotes, origin of tetrapods, and the Permian mass extinction. Briefly describe the significance of each event. You can also add more events to your time line as you study.



Go to Mastering Biology

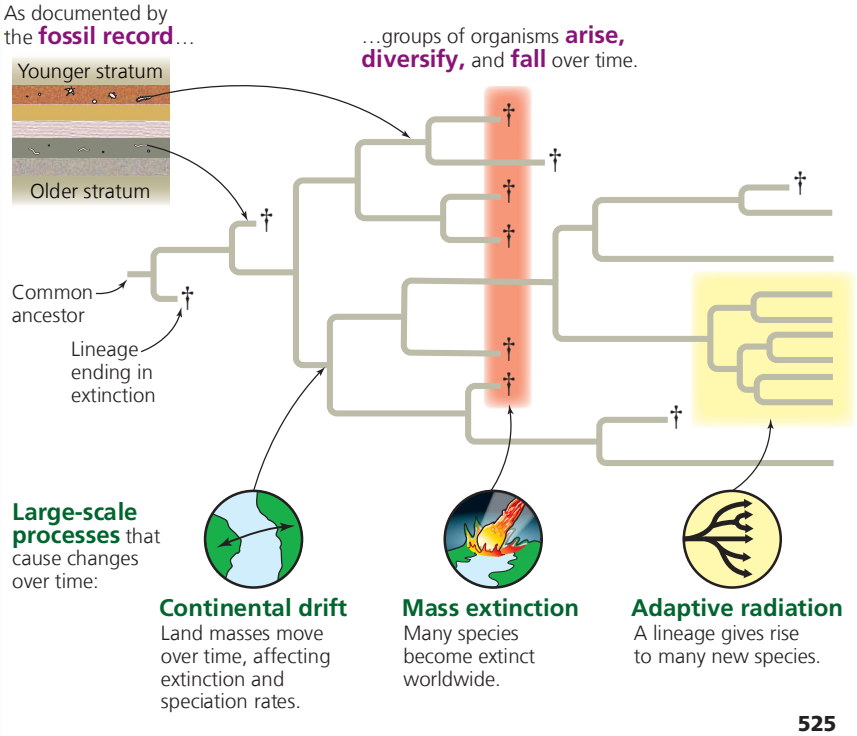
For Students (in eText and Study Area)
- Get Ready for Chapter 25
- Figure 25.10 Walkthrough: Serial Endosymbiosis
- HHMI Video: The Making of the Fittest

For Instructors to Assign (in Item Library)
- Tutorial: Visualizing the Scale of Geologic Time
- HHMI Video: The Day the Mesozoic Died



Figure 25.1 In the 1870s, researchers working in the searing heat of the Sahara Desert were startled to discover fossils of ancient whales. These fossils were spectacular not only for where they were found, but also for documenting the transition from life on land to life in the sea—just one example of the sweeping changes seen in the history of life on Earth.

How has life on Earth changed over time?



The whale fossils discovered in the Sahara Desert (see Figure 25.1) are one example of evidence that past organisms were very different from those presently living. The sweeping changes in life on Earth as revealed by such fossils illustrate **macroevolution**, the broad pattern of evolution above the species level. Examples of macroevolutionary change include the emergence of terrestrial vertebrates through a series of speciation events, the impact of mass extinctions on biodiversity, and the origin of key adaptations such as flight.

Taken together, such changes provide a grand view of the evolutionary history of life. We'll examine that history in this chapter, beginning with a discussion of hypotheses regarding the origin of life. This is the most speculative topic of the entire unit, because no fossil evidence of that seminal episode exists.

CONCEPT 25.1

Conditions on early Earth made the origin of life possible

Direct evidence of life on early Earth comes from fossils of microorganisms that lived 3.5 billion years ago. But how did the first living cells appear? Observations and experiments in chemistry, geology, and physics have led scientists to propose one scenario that we'll examine here. They hypothesize that chemical and physical processes could have produced simple cells through a sequence of four main stages:

1. The abiotic (nonliving) synthesis of small organic molecules, such as amino acids and nitrogenous bases
2. The joining of these small molecules into macromolecules, such as proteins and nucleic acids
3. The packaging of these molecules into **protocells**, droplets with membranes that maintained an internal chemistry different from that of their surroundings
4. The origin of self-replicating molecules that eventually made inheritance possible

Though speculative, this scenario leads to predictions that can be tested in the laboratory. In this section, we'll examine some of the evidence for each stage.

Synthesis of Organic Compounds on Early Earth

Our planet formed 4.6 billion years ago, condensing from a vast cloud of dust and rocks that surrounded the young sun. For its first few hundred million years, Earth was bombarded by huge chunks of rock and ice left over from the formation of the solar system. The collisions generated so much heat that all of the available water was vaporized, preventing the formation of seas and lakes.

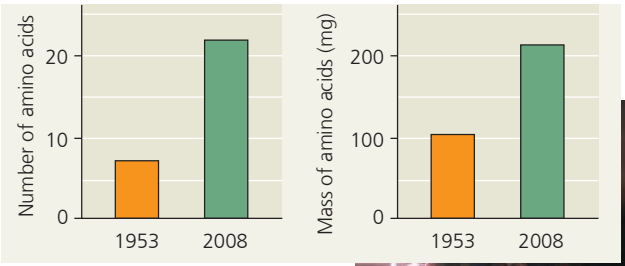
This massive bombardment ended 4 billion years ago, setting the stage for the origin of life. The first atmosphere had little oxygen and was likely thick with water vapor, along with compounds released by volcanic eruptions, such as nitrogen and its oxides, carbon dioxide, methane, ammonia, and hydrogen. As Earth cooled, the water vapor condensed into oceans, and much of the hydrogen escaped into space.

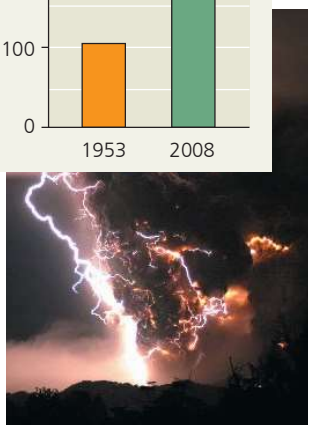
During the 1920s, Russian chemist A. I. Oparin and British scientist J. B. S. Haldane independently hypothesized that Earth's early atmosphere was a reducing (electron-adding) environment, in which organic compounds could have formed from simpler molecules. The energy for this synthesis could have come from lightning and UV radiation. Haldane suggested that the early oceans were a solution of organic molecules, a "primitive soup" from which life arose.

In 1953, Stanley Miller, working with Harold Urey at the University of Chicago, tested the Oparin-Haldane hypothesis by creating laboratory conditions comparable to those that scientists at the time thought existed on early Earth (see Figure 4.2). His apparatus yielded a variety of amino acids found in organisms today, along with other organic compounds. Many laboratories have since repeated Miller's classic experiment using different recipes for the atmosphere, some of which also produced organic compounds.

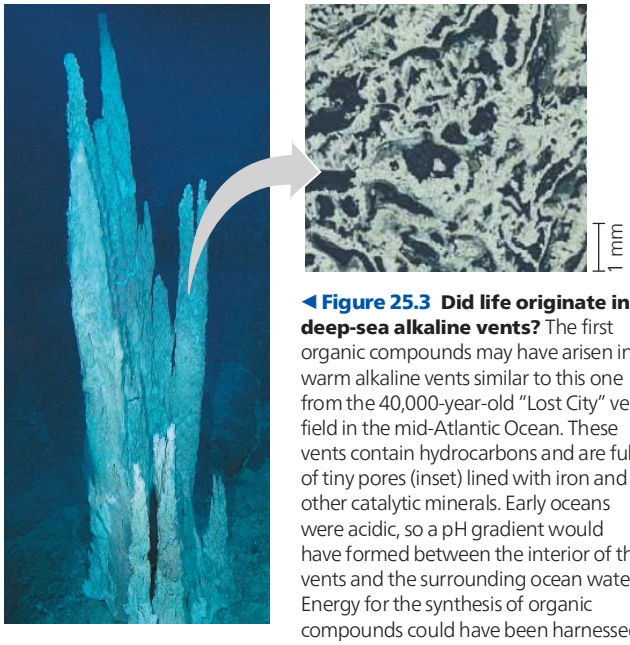
However, some evidence suggests that the early atmosphere was made up primarily of nitrogen and carbon dioxide and was neither reducing nor oxidizing (electron removing). Recent Miller/Urey-type experiments using such "neutral" atmospheres have also produced organic molecules. In addition, small pockets of the early atmosphere, such as those near the openings of volcanoes, may have been reducing. Perhaps the first organic compounds formed near volcanoes. In a test of this hypothesis **(Figure 25.2)**, researchers used modern equipment

▼ Figure 25.2 Amino acid synthesis in a simulated volcanic eruption. In addition to his classic 1953 study, Miller also conducted an experiment simulating a volcanic eruption. In a 2008 reanalysis of those results, researchers found that far more amino acids were produced under simulated volcanic conditions than were produced in the conditions of the classic 1953 study.





MAKE CONNECTIONS *Explain how more than 20 amino acids could have been obtained in the 2008 study. (See Concept 5.4.)*



◀ Figure 25.3 Did life originate in deep-sea alkaline vents? The first organic compounds may have arisen in warm alkaline vents similar to this one from the 40,000-year-old "Lost City" vent field in the mid-Atlantic Ocean. These vents contain hydrocarbons and are full of tiny pores (inset) lined with iron and other catalytic minerals. Early oceans were acidic, so a pH gradient would have formed between the interior of the vents and the surrounding ocean water. Energy for the synthesis of organic compounds could have been harnessed from this pH gradient.

to reanalyze molecules that Miller had saved from one of his experiments. They found that numerous amino acids had formed under conditions that simulated a volcanic eruption.

Another hypothesis is that organic compounds were first produced in deep-sea **hydrothermal vents**, areas on the seafloor where heated water and minerals gush from Earth's interior into the ocean. Some of these vents, known as "black smokers," release water so hot (300–400°C) that organic compounds formed there may have been unstable. But other deep-sea vents, called **alkaline vents**, release water that has a high pH (9–11) and is warm (40–90°C) rather than hot, an environment that may have been more suitable for the origin of life **(Figure 25.3)**.

Studies related to the volcanic atmosphere and alkaline vent hypotheses show that the abiotic synthesis of organic molecules is possible under various conditions. Another source of organic molecules may have been meteorites. For example, fragments of the Murchison meteorite, a 4.5-billion-year-old rock that landed in Australia in 1969, contain more than 80 amino acids, some in large amounts. These amino acids cannot be contaminants from Earth because they consist of an equal mix of D and L isomers (see Figure 4.7). Organisms make and use only L isomers, with a few rare exceptions. Studies have shown that the Murchison meteorite also contained other key organic molecules, including lipids, simple sugars, and nitrogenous bases such as uracil.

Abiotic Synthesis of Macromolecules

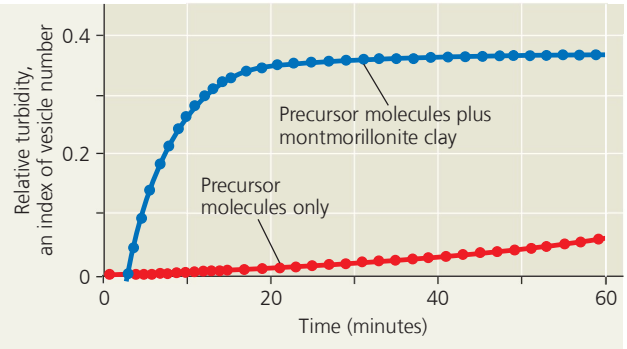
The presence of small organic molecules, such as amino acids and nitrogenous bases, is not sufficient for the emergence of life as we know it. Every cell has many types of macromolecules, including enzymes and other proteins and the nucleic acids needed for self-replication. Could such macromolecules have formed on early Earth? A 2016 study demonstrated that one key step, the abiotic synthesis of RNA's two purine bases, adenine (A) and guanine (G), can occur spontaneously from simple precursor molecules; the abiotic synthesis of the smaller cytosine (C) and uracil (U) bases was accomplished in 2009. In addition, by dripping solutions of amino acids or RNA nucleotides onto hot sand, clay, or rock, researchers have produced polymers of these molecules. The polymers formed spontaneously, without the help of enzymes or ribosomes. Unlike proteins, the amino acid polymers are a complex mix of linked and cross-linked amino acids. Still, it is possible that such polymers acted as weak catalysts for a variety of chemical reactions on early Earth.

Protocells

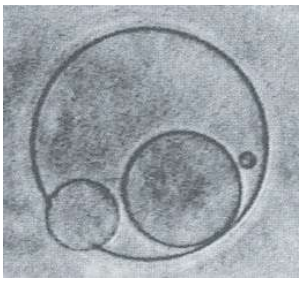
All organisms must be able to carry out both reproduction and energy processing (metabolism). DNA molecules carry genetic information, including the instructions needed to replicate themselves accurately during reproduction. But DNA replication requires elaborate enzymatic machinery, along with an abundant supply of nucleotide building blocks provided by the cell's metabolism. This suggests that self-replicating molecules and a metabolic source of building blocks may have appeared together in early protocells. The necessary conditions may have been met in *vesicles*, fluid-filled compartments enclosed by a membrane-like structure. Recent experiments show that abiotically produced vesicles can exhibit certain properties of life, including simple reproduction and metabolism, as well as the maintenance of an internal chemical environment different from that of their surroundings **(Figure 25.4)**.

For example, vesicles can form spontaneously when lipids or other organic molecules are added to water. When this occurs, molecules that have both a hydrophobic region and a hydrophilic region can organize into a bilayer similar to the lipid bilayer of a plasma membrane. Adding substances such as *montmorillonite*, a soft mineral clay produced by the weathering of volcanic ash, greatly increases the rate of vesicle self-assembly (see Figure 25.4a). This clay, which is thought to have been common on early Earth, provides surfaces on which organic molecules become concentrated, increasing the likelihood that the molecules will react with each other and form vesicles. Abiotically produced vesicles can "reproduce" on their own (see Figure 25.4b), and they can increase in size ("grow") without dilution of their contents. Vesicles also can absorb montmorillonite particles, including those on which RNA and other organic molecules have become attached (see Figure 25.4c). Finally, experiments have shown that some vesicles have a selectively permeable bilayer and can perform metabolic reactions using an external source of reagents—another important prerequisite for life.

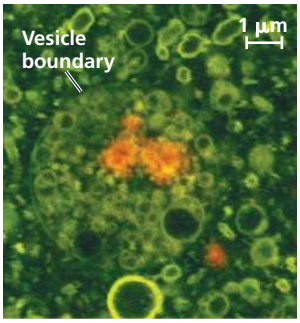
▼ Figure 25.4 Features of abiotically produced vesicles.



(a) Self-assembly. The presence of montmorillonite clay greatly increases the rate of vesicle self-assembly.



(b) Reproduction. Vesicles can divide on their own, as in this vesicle "giving birth" to smaller vesicles (LM).



(c) Absorption of RNA. This vesicle has incorporated montmorillonite clay particles coated with RNA (orange).

MAKE CONNECTIONS *Explain how molecules with both a hydrophobic region and a hydrophilic region can self-assemble into a bilayer when in water. (See Concept 5.3.)*

Self-Replicating RNA

The first genetic material was most likely RNA, not DNA. RNA plays a central role in protein synthesis, but it can also function as an enzyme-like catalyst (see Concept 17.3). Such RNA catalysts are called **ribozymes**. Some ribozymes can make complementary copies of short pieces of RNA, provided that they are supplied with nucleotide building blocks.

Natural selection on the molecular level has produced ribozymes capable of self-replication in the laboratory. How does this occur? Unlike double-stranded DNA, which takes the form of a uniform helix, single-stranded RNA molecules assume a variety of specific three-dimensional shapes mandated by their nucleotide sequences. In a given environment, RNA molecules with certain nucleotide sequences may have shapes that enable them to replicate faster and with fewer errors than other sequences. The RNA molecule with the greatest ability to replicate itself will leave the most descendant molecules. Occasionally, a copying error will result in a molecule with a shape that is even more adept at self-replication. Similar selection events may have occurred on early Earth. Thus, life as we know it may have been preceded by an "RNA world," in which small RNA molecules were able to replicate and to store genetic information about the vesicles that carried them.

Recently, Dr. Jack Szostak and colleagues at Harvard University succeeded in building a vesicle in which copying of a template strand of RNA could occur—a key step toward constructing a vesicle with self-replicating RNA. On early Earth, a vesicle with such self-replicating, catalytic RNA would differ from its many neighbors that lacked such molecules. If that vesicle could grow, split, and pass its RNA molecules to its "daughters," the daughters would be protocells. Although the first such protocells likely carried only limited amounts of genetic information, specifying only a few properties, their inherited characteristics could have been acted on by natural selection. The most successful of the early protocells would have increased in number because they could exploit their resources effectively and pass their abilities on to subsequent generations.

Once RNA sequences that carried genetic information appeared in protocells, many additional changes would have been possible. For example, RNA could have provided the template on which DNA nucleotides were assembled. Double-stranded DNA is a more chemically stable repository for genetic information than is the more fragile RNA. DNA also can be replicated more accurately. Accurate replication was advantageous as genomes grew larger through gene duplication and other processes and as more properties of the protocells became coded in genetic information. Once DNA appeared, the stage was set for a blossoming of new forms of life—a change we see documented in the fossil record.

Mastering Biology
Interview with Jack Szostak: Studying the origin of life



CONCEPT CHECK 25.1

1. What hypothesis did Miller test in his classic experiment?
2. How would the appearance of protocells have represented a key step in the origin of life?
3. **MAKE CONNECTIONS** In changing from an "RNA world" to today's "DNA world," genetic information must have flowed from RNA to DNA. After reviewing Figures 17.4 and 19.9, suggest how this could have occurred. Does such a flow occur today?

For suggested answers, see Appendix A.

CONCEPT 25.2

The fossil record documents the history of life

Starting with the earliest traces of life, the fossil record opens a window into the world of long ago and provides glimpses of the evolution of life over billions of years. In this section, we'll examine fossils as a form of scientific evidence: how fossils



▶ Figure 25.5 A gallery of fossil types. (a) Sedimentary rock. Most fossils are found in sedimentary rocks, such as this plant fossil. **(b) Mineralized organic matter.** Some fossils, such as this petrified tree trunk, form as minerals seep into and replace organic matter. **(c) Trace fossils.** Footprints, burrows, or other traces of an organism's activities can be preserved in the fossil record. **(d) Amber.** Entire organisms are sometimes found preserved in hardened resin from a tree. **(e) Frozen soil, ice, and acid bogs.** Rarely, frozen soil, ice, or an acid bog can preserve the body of larger organisms, such as this wolf pup.

form, how scientists date and interpret them, and what they can and cannot tell us about changes in the history of life.

The Fossil Record

Sedimentary rocks are the richest source of fossils. As a result, the fossil record is based primarily on the sequence in which fossils have accumulated in sedimentary rock layers, called *strata* (see Figure 22.3). Useful information is also provided by other types of fossils, such as insects preserved in amber (fossilized tree sap) and mammals frozen in soil **(Figure 25.5)**.

The fossil record shows that there have been great changes in the kinds of organisms on Earth at different points in time. Many past organisms were unlike organisms living today, and many organisms that once were common are now extinct. As we'll see later in this section, fossils also document how new groups of organisms arose from previously existing ones.

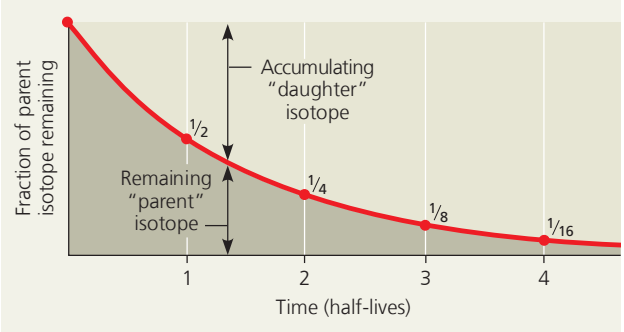
As substantial and significant as the fossil record is, keep in mind that it is an incomplete chronicle of evolution. Many of Earth's organisms did not die in the right place and time to be preserved as fossils. Of the fossils that were formed, many were destroyed by later geologic processes, and only a fraction of the others have been discovered. As a result, the known fossil record is biased in favor of species that existed for a long time, were abundant and widespread in certain kinds of environments, and had hard shells, skeletons, or other parts that facilitated their fossilization. Even with its limitations, however, the fossil record is a remarkably detailed account of biological change over the vast scale of geologic time. Furthermore, as shown by recently unearthed fossils of whale ancestors with hind limbs (see Figure 22.19 and Figure 25.1), gaps in the fossil record continue to be filled by new discoveries.

How Rocks and Fossils Are Dated

Fossils provide valuable data for reconstructing the history of life, but only if we can determine where they fit in that story. While the order of fossils in rock strata tells us the sequence in which the fossils were laid down—their relative ages—it does not tell us their actual ages. Examining the relative positions of fossils is like peeling off layers of wallpaper in an old house. You can infer the sequence in which the layers were applied, but not the year each layer was added.

How can we determine the age of a fossil? One of the most common techniques is **radiometric dating**, which is based on the decay of radioactive isotopes (see Concept 2.2). In this process, a radioactive "parent" isotope decays to a "daughter" isotope at a characteristic rate. The rate of decay is expressed by the **half-life**, the time required for 50% of the parent

▼ **Figure 25.6** **Radiometric dating.** In this diagram, each unit of time represents one half-life of a radioactive isotope.



DRAW IT *Relabel the x-axis of this graph in years to illustrate the radioactive decay of uranium-238 (half-life = 4.5 billion years).*

isotope to decay **(Figure 25.6)**. Each type of radioactive isotope has a characteristic half-life, which is not affected by temperature, pressure, or other environmental variables. For example, carbon-14 decays relatively quickly; its half-life is 5,730 years. Uranium-238 decays slowly; its half-life is 4.5 billion years.

Fossils contain isotopes of elements that accumulated in the organisms when they were alive. For example, a living organism contains the most common carbon isotope, carbon-12, as well as a radioactive isotope, carbon-14. When the organism dies, it stops accumulating carbon, and the amount of carbon-12 in its tissues does not change over time. However, the carbon-14 that it contains at the time of death slowly decays into another element, nitrogen-14. Thus, by measuring the ratio of carbon-14 to carbon-12 in a fossil, we can determine the fossil's age. This method works for fossils up to about 75,000 years old; fossils older than that contain too little carbon-14 to be detected with current techniques. Radioactive isotopes with longer half-lives are used to date older fossils.

Determining the age of these older fossils in sedimentary rocks can be challenging. Organisms do not use radioisotopes with long half-lives, such as uranium-238, to build their bones or shells. In addition, sedimentary rocks are often composed of sediments of differing ages. Although we cannot date these older fossils directly, an indirect method can be used to infer the age of fossils that are sandwiched between two layers of volcanic rock. As lava cools into volcanic rock, radioisotopes from the surrounding environment become trapped in the newly formed rock. Some of the trapped radioisotopes have long half-lives, allowing geologists to estimate the ages of ancient volcanic rocks. If two volcanic layers surrounding fossils are found to be 525 million and 535 million years old, for example, then the fossils are roughly 530 million years old.

The study of fossils has helped geologists establish a geologic record: a standard time scale that divides Earth's history into four eons and further subdivisions **(Table 25.1)**. We'll describe key events that occurred during these different time periods in Concept 25.3.

Table 25.1 The Geologic Record

Eon	Era	Period	Epoch	Age (Millions of Years Ago)
Phanerozoic	Cenozoic	Quaternary	Holocene	0.01
			Pleistocene	2.6
		Neogene	Pliocene	5.3
			Miocene	23
		Paleogene	Oligocene	33.9
			Eocene	56
			Paleocene	66
	Mesozoic	Cretaceous		145
		Jurassic		201
		Triassic		252
	Paleozoic	Permian		299
		Carboniferous		359
		Devonian		419
		Silurian		444
		Ordovician		485
		Cambrian		541
Proterozoic	Neoproterozoic	Ediacaran		635
				1,000
Archaean				2,500
				4,000
Hadean				Approx. 4,600

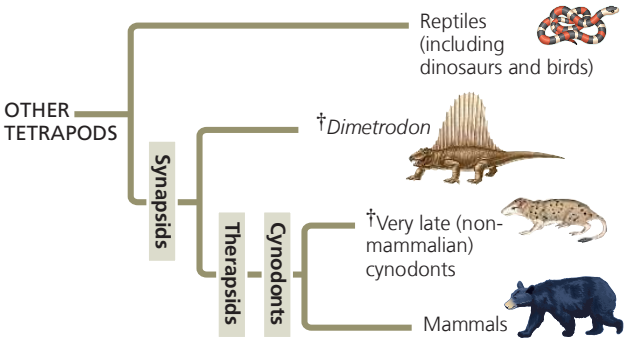
The Origin of New Groups of Organisms

Some fossils document the origin of new groups of organisms. Such fossils are central to our understanding of evolution; they illustrate how new features arise and how long it takes for such changes to occur. We'll examine one such case here and in **Figure 25.7**: the origin of mammals.

Along with amphibians and reptiles, mammals belong to the group of animals called *tetrapods* (from the Greek *tetra*, four, and *pod*, foot), named for having four limbs. Mammals have a number of unique anatomical features that fossilize readily, allowing scientists to trace their origin. For example, the lower jaw is composed of one bone (the dentary) in mammals but several bones in other tetrapods. In addition, the lower and upper jaws in mammals hinge between a different set of bones than in other tetrapods. Mammals also have a unique set of three bones that transmit sound in the middle ear, the hammer, anvil, and stirrup, whereas other tetrapods have only one such bone, the stirrup (see Concept 34.6). Finally, the teeth of mammals are differentiated into incisors (for tearing), canines (for piercing), and the multi-pointed premolars and molars

▼ Figure 25.7 Exploring the Origin of Mammals

Over the course of 120 million years, mammals originated gradually from a group of tetrapods called synapsids. Shown here are a few of the many fossil organisms whose morphological features represent intermediate steps between living mammals and their early synapsid ancestors. The evolutionary context of the origin of mammals is shown in the tree diagram at right (the dagger symbol † indicates extinct lineages).

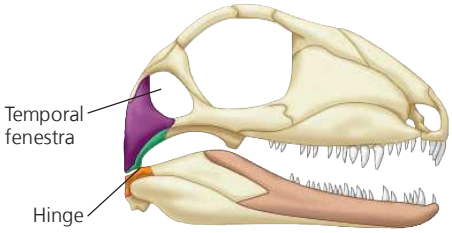


Key to skull bones

Articular
Quadrate
Dentary
Squamosal

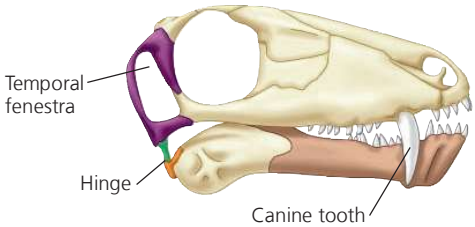
Synapsid (300 mya)

Early synapsids had multiple bones in the lower jaw and single-pointed teeth. The jaw hinge was formed by the articular and quadrate bones. Early synapsids also had an opening called the *temporal fenestra* behind the eye socket. Powerful cheek muscles for closing the jaws probably passed through the temporal fenestra. Over time, this opening enlarged and moved in front of the hinge between the lower and upper jaws, thereby increasing the power and precision with which the jaws could be closed (much as moving a doorknob away from the hinge makes a door easier to close).



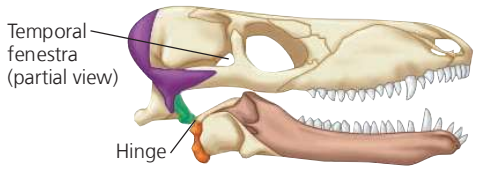
Therapsid (280 mya)

Later, a group of synapsids called therapsids appeared. Therapsids had large dentary bones, long faces, and the first examples of specialized teeth, large canines. These trends continued in a group of therapsids called cynodonts.



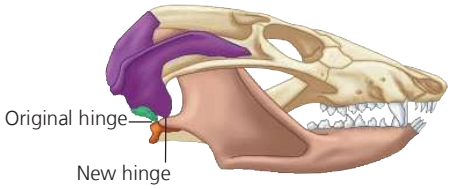
Early cynodont (260 mya)

In early cynodont therapsids, the dentary was the largest bone in the lower jaw, the temporal fenestra was large and positioned forward of the jaw hinge, and teeth with several cusps first appeared (not visible in the diagram). As in earlier synapsids, the jaw had an articular-quadrate hinge.



Later cynodont (220 mya)

Later cynodonts had teeth with complex cusp patterns, and their lower and upper jaws hinged in two locations: They retained the original articular-quadrate hinge and formed a new, second hinge between the dentary and squamosal bones. (The temporal fenestra is not visible in this or the below cynodont skull at the angles shown.)



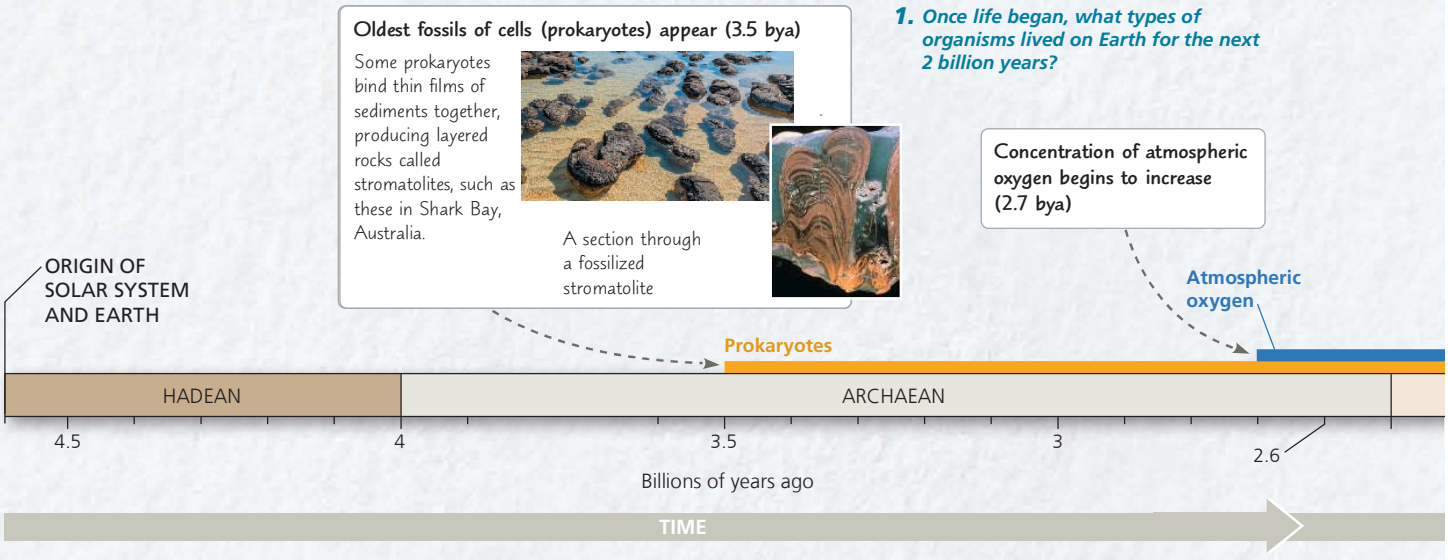
Very late cynodont (195 mya)

In some very late (nonmammalian) cynodonts and early mammals, the original articular-quadrate hinge was lost, leaving the dentary-squamosal hinge as the only hinge between the lower and upper jaws, as in living mammals. The articular and quadrate bones migrated into the ear region (not shown), where they functioned in transmitting sound. In the mammal lineage, these two bones later evolved into the familiar hammer (malleus) and anvil (incus) bones of the ear.

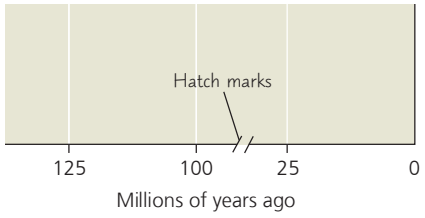


▼ Figure 25.8 VISUALIZING THE SCALE OF GEOLOGIC TIME

Geologic time is so vast that it can be difficult to visualize when key events in the history of life on Earth occurred. In this time line, time runs from left to right, from 4.6 billion years ago to the present. The fossils along the top illustrate representative organisms from different points in time.



The large time line in this figure shows all of geologic time to scale on an unbroken time line, but sometimes it is helpful to "break" a time line to limit a figure's size and highlight key details. As shown at right, hatch marks are often used to represent such an interruption.



2. Look for a figure in this chapter that uses hatch marks on one of its axes. Explain what the hatch marks represent in that figure.

(for crushing and grinding). In contrast, the teeth of other tetrapods usually consist of a row of undifferentiated, single-pointed teeth.

As detailed in Figure 25.7, the fossil record shows that the unique features of mammalian jaws and teeth evolved gradually, in a series of steps. Keep in mind that the figure includes just a few examples of the fossil skulls that document the origin of mammals. If all the known fossils in the sequence were arranged by shape and placed side by side, their features would blend smoothly from one group to the next. Some of these fossils would reflect how the features of a group that dominates life today, the mammals, gradually arose in a previously existing group, the cynodonts. Others would reveal side branches on the tree of life—groups of organisms that thrived for millions of years but ultimately left no descendants that survive today.

CONCEPT CHECK 25.2

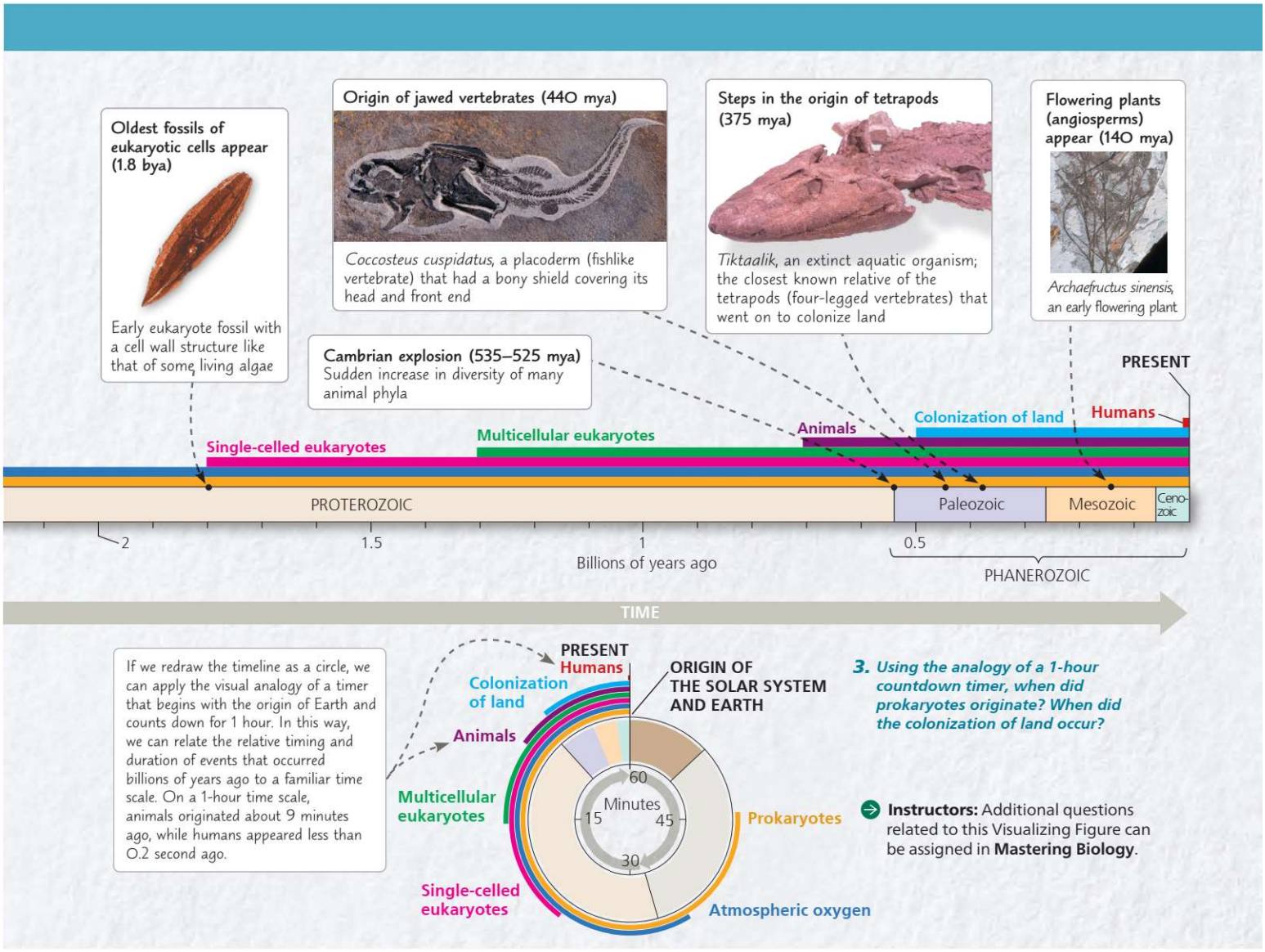
1. Describe an example from the fossil record that shows how life has changed over time.
2. **WHAT IF?** A fossilized skull you unearthed has a carbon-14/carbon-12 ratio about $1/16$ that of the skulls of present-day animals. Approximately how many years old is the fossilized skull?

For suggested answers, see Appendix A.

CONCEPT 25.3

Key events in life's history include the origins of unicellular and multicellular organisms and the colonization of land

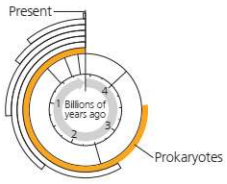
The first three eons in the geologic record—the Hadean, the Archaean, and the Proterozoic—together lasted about



4 billion years. The Phanerozoic eon, roughly the last half billion years, encompasses most of the time that animals have existed on Earth. It is divided into three eras: the Paleozoic, Mesozoic, and Cenozoic. Each era represents a distinct age in the history of Earth and its life. For example, the Mesozoic era is sometimes called the "age of reptiles" because of its abundance of reptilian fossils, including those of dinosaurs. The boundaries between the eras correspond to major extinction events, when many forms of life disappeared and were replaced by forms that evolved from the survivors.

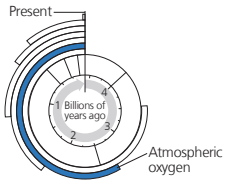
As we've seen, the fossil record provides a sweeping overview of the history of life over geologic time. Here we will focus on a few major events in that history, returning to study the details in Unit Five. **Figure 25.8** will help you visualize how long ago these key events occurred against the vast backdrop of geologic time.

The First Single-Celled Organisms



Earth's first organisms were single-celled prokaryotes that lived in the ocean. The earliest direct evidence of these organisms, dating from 3.5 billion years ago, comes from fossilized stromatolites. **Stromatolites** are layered rocks that form when certain prokaryotes bind thin films of sediment together. Stromatolites and other early prokaryotes were Earth's sole inhabitants for about 1.5 billion years. As we will see, these prokaryotes transformed life on our planet.

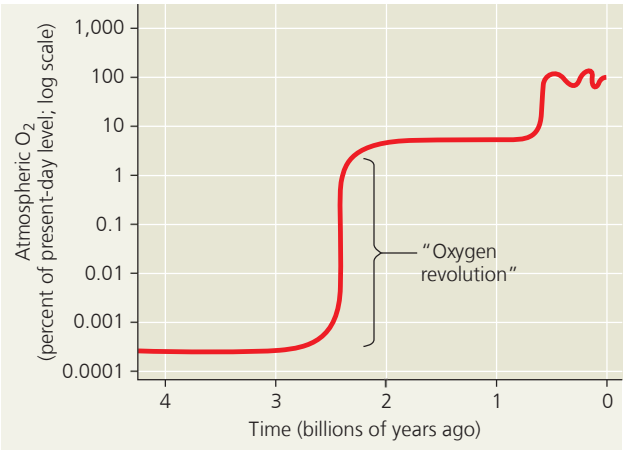
Photosynthesis and the Oxygen Revolution



Most atmospheric oxygen gas (O_2) is of biological origin, produced during the water-splitting step of photosynthesis. When oxygenic photosynthesis first evolved—in photosynthetic prokaryotes similar to today's cyanobacteria—the free O_2 it produced probably dissolved in the surrounding water until it reached a high enough concentration to react with elements dissolved in water, including iron. This would have caused the iron to precipitate as iron oxide, which accumulated as sediments. These sediments were compressed into banded iron formations, red layers of rock containing iron oxide that are a source of iron ore today. Once all of the dissolved iron had precipitated, additional O_2 dissolved in the water until the seas and lakes became saturated with O_2. After this occurred, the O_2 finally began to "gas out" of the water and enter the atmosphere. This change left its mark in the rusting of iron-rich terrestrial rocks, a process that began about 2.7 billion years ago.

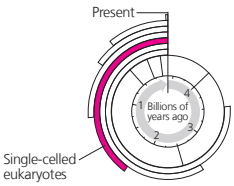
As shown in **Figure 25.9**, the amount of atmospheric O_2 increased gradually from about 2.7 to 2.4 billion years ago, but then shot up relatively rapidly to between 1% and 10% of its present level. This "oxygen revolution" had an enormous impact on life. In some of its chemical forms, oxygen attacks chemical bonds and can inhibit enzymes and damage cells. As a result, the rising concentration of atmospheric O_2 probably doomed many prokaryotic groups. Some species survived in habitats that remained anaerobic, where we find their descendants living today (see Concept 27.4). Among other survivors, diverse adaptations to the changing atmosphere evolved, including cellular respiration, which uses O_2 in the process of harvesting the energy stored in organic molecules.

▼ Figure 25.9 The rise of atmospheric oxygen. Chemical analyses of ancient rocks have enabled this reconstruction of atmospheric oxygen levels during Earth's history.



The rise in atmospheric O_2 levels left a huge imprint on the history of life. A few hundred million years later, another fundamental change occurred: the origin of the eukaryotic cell.

The First Eukaryotes



The oldest widely accepted fossils of eukaryotes are of single-celled organisms that lived 1.8 billion years ago. Recall that eukaryotic cells have more complex organization than prokaryotic cells: Eukaryotic cells have a nuclear envelope, mitochondria, endoplasmic reticulum, and other internal structures that prokaryotes lack. Also, unlike prokaryotic cells, eukaryotic cells have a well-developed cytoskeleton, a feature that enables eukaryotic cells to change their shape and thereby surround and engulf other cells.

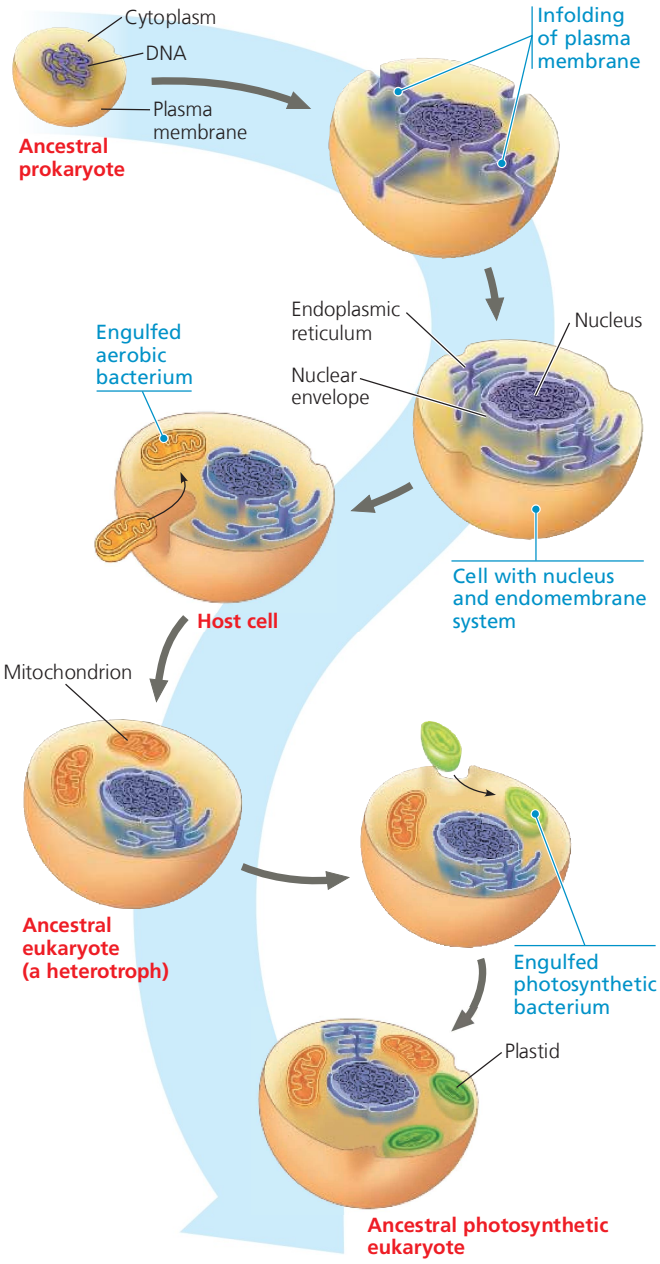
How did the eukaryotes evolve from their prokaryotic ancestors? Current evidence indicates that the eukaryotes originated by **endosymbiosis** when a prokaryotic cell engulfed a small cell that would evolve into an organelle found in all eukaryotes, the mitochondrion. The small, engulfed cell is an example of an *endosymbiont*, a cell that lives within another cell, called the *host cell*. The prokaryotic ancestor of the mitochondrion probably entered the host cell as undigested prey or an internal parasite. Though such a process may seem unlikely, scientists have directly observed cases in which endosymbionts that began as prey or parasites developed a mutually beneficial relationship with a host in as little as five years.

By whatever means the relationship began, we can hypothesize how the symbiosis could have become beneficial. For example, in a world that was becoming increasingly aerobic, a host that was itself an anaerobe would have benefited from endosymbionts that could make use of the oxygen. Over time, the host and endosymbionts would have become a single organism, its parts inseparable. Although all eukaryotes have mitochondria or remnants of these organelles, they do not all have plastids (a general term for chloroplasts and related organelles). Thus, the **serial endosymbiosis** hypothesis supposes that mitochondria evolved before plastids through a sequence of endosymbiotic events. As shown in **Figure 25.10**, both mitochondria and plastids are thought to have descended from bacterial cells. The original host—the cell that engulfed the bacterium whose descendants gave rise to the mitochondrion—is thought to have been an archaean or a close relative of the archaea.

A great deal of evidence supports the endosymbiotic origin of mitochondria and plastids:

- The inner membranes of both organelles have enzymes and transport systems that are homologous to those found in the plasma membranes of living bacteria.

▼ Figure 25.10 A hypothesis for the origin of mitochondria and plastids through serial endosymbiosis. The proposed host cell was an archaean or a close relative of the archaea. The proposed ancestors of mitochondria were aerobic, heterotrophic bacteria, while the proposed ancestors of plastids were photosynthetic bacteria. In this figure, the arrows represent change over evolutionary time.



Mastering Biology Figure Walkthrough

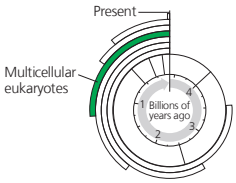
- Mitochondria and plastids replicate by a splitting process that is similar to that of certain bacteria. In addition, each of these organelles contains circular DNA molecules that, like the chromosomes of bacteria, are not associated with histones or large amounts of other proteins.
- As might be expected of organelles descended from free-living organisms, mitochondria and plastids also have the cellular machinery (including ribosomes) needed to transcribe and translate their DNA into proteins.
- Finally, in terms of size, RNA sequences, and sensitivity to certain antibiotics, the ribosomes of mitochondria and plastids are more similar to bacterial ribosomes than they are to the cytoplasmic ribosomes of eukaryotic cells.

In Concept 28.1, we'll return to the origin of eukaryotes, focusing on what genomic data have revealed about the prokaryotic lineages that gave rise to the host and endosymbiont cells.

The Origin of Multicellularity

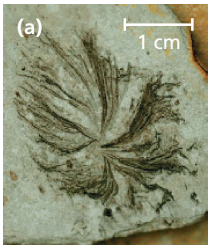
An orchestra can play a greater variety of musical compositions than a violin soloist can; the increased complexity of the orchestra makes more variations possible. Likewise, the origin of structurally complex eukaryotic cells sparked the evolution of greater morphological diversity than was possible for the simpler prokaryotic cells. After the first eukaryotes appeared, a great range of unicellular forms evolved, giving rise to the diversity of single-celled eukaryotes that continue to flourish today. Another wave of diversification also occurred: Some single-celled eukaryotes gave rise to multicellular forms, whose descendants include a variety of algae, plants, fungi, and animals.

Early Multicellular Eukaryotes



Fossil evidence and DNA sequence data suggest that multicellular eukaryotes emerged about 1.3 billion years ago. The oldest known fossils of multicellular eukaryotes that can be resolved taxonomically are of relatively small red algae that lived 1.2 billion years ago. Larger and more diverse multicellular eukaryotes do not appear in the fossil record until about 600 million years ago **(Figure 25.11)**. These fossils, referred to as the

▼ Figure 25.11 Life becomes large. Fossils from the Ediacaran period document the oldest known macroscopic eukaryotes, such as **(a)** *Doushantuophyton*, an alga that lived 600 mya, and **(b)** *Kimberella*, a mollusc (or close relative) that lived 560 mya.

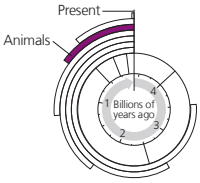




Ediacaran biota, were of mostly soft-bodied organisms—some over 1 m long—that lived from 635 to 541 million years ago (mya). The Ediacaran biota included both algae and animals, along with various organisms of unknown taxonomic affinity.

The rise of large eukaryotes in the Ediacaran period represents an enormous change in the history of life. Before that time, Earth was a microbial world: Its only inhabitants were single-celled prokaryotes and eukaryotes, along with an assortment of microscopic, multicellular eukaryotes. As the diversification of the Ediacaran biota came to a close about 541 million years ago, the stage was set for another, even more spectacular burst of evolutionary change: the "Cambrian explosion."

The Cambrian Explosion

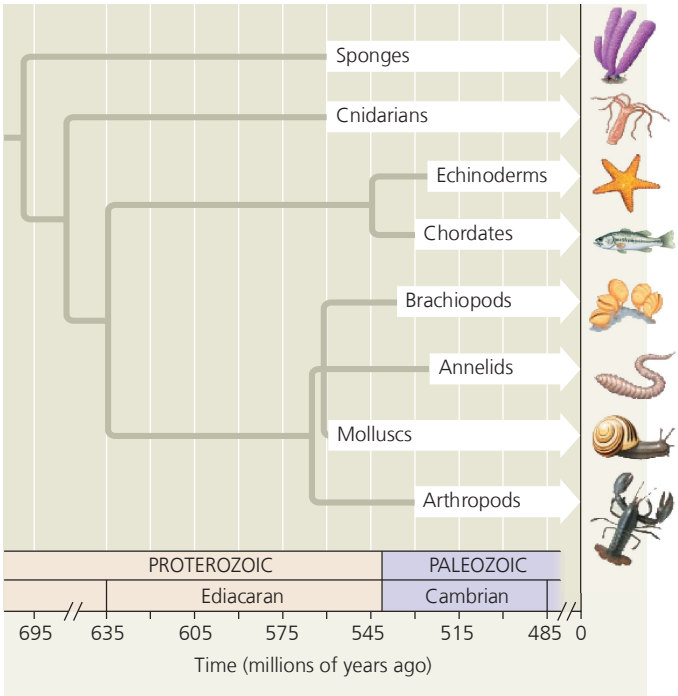


Many present-day animal phyla appear suddenly in fossils formed 535–525 million years ago, early in the Cambrian period. This phenomenon is referred to as the **Cambrian explosion**. Fossils of several animal groups—sponges, cnidarians (sea anemones and their relatives), and molluscs (snails, clams, and their relatives)—appear in even older rocks dating from the late Proterozoic **(Figure 25.12)**.

Prior to the Cambrian explosion, all large animals were soft-bodied. The fossils of large pre-Cambrian animals reveal little evidence of predation. Instead, these animals appear to have been grazers (feeding on algae), filter feeders, or scavengers, not hunters. The Cambrian explosion changed all of that. In a relatively short period of time (10 million years), predators over 1 m in length emerged that had claws and other features for capturing prey; simultaneously, new defensive adaptations, such as sharp spines and heavy body armor, appeared in their prey.

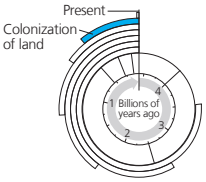
Although the Cambrian explosion had an enormous impact on life on Earth, it appears that many animal phyla originated long before that time. Recent DNA analyses suggest that sponges had evolved by 700 million years ago; such analyses also indicate that the common ancestor of arthropods, chordates, and other animal phyla that radiated during the Cambrian explosion lived 670 million years ago. Researchers have unearthed 710-million-year-old sediments containing steroids indicative of a particular group of sponges—a finding that supports the molecular data. In contrast, the oldest macroscopic fossils of animals date from 560 million years ago and include *Kimberella*, shown in Figure 25.11. Overall, fossils and DNA analyses suggest that animals originated about 700 million years ago and then remained small for over 100 million years—until they diversified explosively during the Cambrian and beyond.

▼ Figure 25.12 Appearance of selected animal groups. The white bars indicate the earliest fossil record of these animal groups.



VISUAL SKILLS *Circle the branch point that represents the most recent common ancestor of chordates and annelids. What is a minimum estimate of that ancestor's age?*

The Colonization of Land

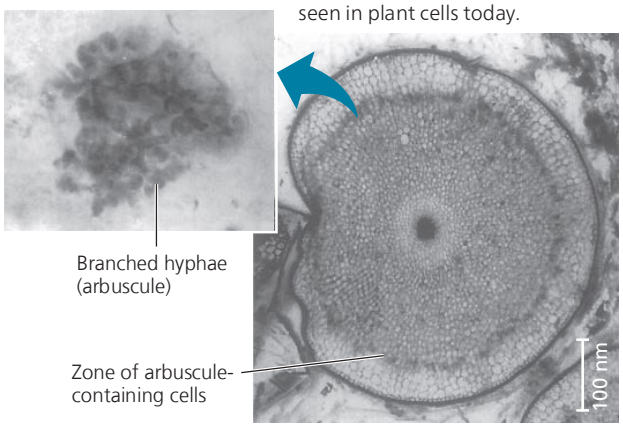


The colonization of land was another milestone in the history of life. There is fossil evidence that some prokaryotes lived on terrestrial surfaces as early as 3.2 billion years ago. However, larger forms of life, such as fungi, plants, and animals, did not begin to colonize land until about 500 million years ago. This gradual evolutionary venture out of aquatic environments was associated with adaptations that made it possible to reproduce on land and that helped prevent dehydration. For example, many plants today have a vascular system for transporting materials internally and a waterproof coating of wax on their leaves that slows the loss of water to the air. Early signs of these adaptations were present 420 million years ago, at which time small plants (about 10 cm high) existed that had a vascular system but lacked true roots or leaves. By 40 million years later, plants had diversified greatly and included trees and many other plants with true roots and leaves.

Plants appear to have colonized land in the company of fungi. Even today, the roots of most plants are associated with fungi that aid in the absorption of water and minerals from the soil (see Concept 31.1). These root fungi (or *mycorrhizae*), in turn, obtain their organic nutrients from the plants. Such mutually beneficial associations of plants and fungi are evident in some of the oldest fossilized plants, dating this relationship back to the early spread of life onto land **(Figure 25.13)**.

Although many animal groups are now represented in terrestrial environments, the most widespread and diverse land

▼ Figure 25.13 An ancient symbiosis. This 405-million-year-old fossil stem (cross section) documents mycorrhizae in the early plant *Aglaophyton major*. The inset shows an enlarged view of a cell containing a branched fungal structure called an arbuscule; the fossil arbuscule resembles those seen in plant cells today.



animals are arthropods (particularly insects and spiders) and tetrapods. Arthropods were among the first animals to colonize land, roughly 450 million years ago. The earliest tetrapods found in the fossil record lived about 365 million years ago and appear to have evolved from a group of lobe-finned fishes (see Concept 34.3). Tetrapods include humans, although we are late arrivals on the scene. The human lineage diverged from other primates around 6–7 million years ago, and our species originated only about 195,000 years ago. If the clock of Earth's history were rescaled to represent an hour, humans appeared less than 0.2 second ago.

Mastering Biology
Interview with Geerat Vermeij: What fossils reveal about the history of life



CONCEPT CHECK 25.3

1. The first appearance of free oxygen in the atmosphere likely triggered a massive wave of extinctions among the prokaryotes of the time. Why?
2. What evidence supports the hypothesis that mitochondria preceded plastids in the evolution of eukaryotic cells?
3. **WHAT IF?** What would a fossil record of life today look like?

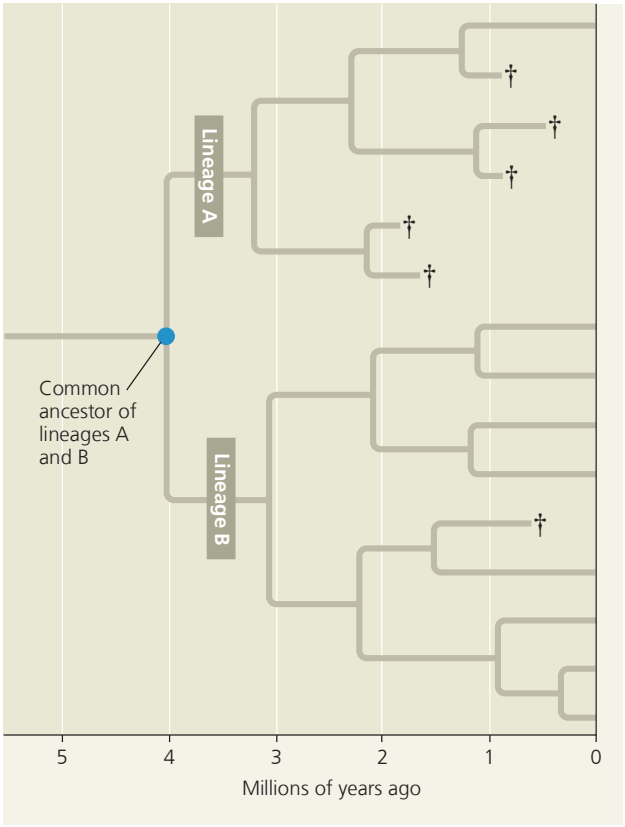
For suggested answers, see Appendix A.

CONCEPT 25.4

The rise and fall of groups of organisms reflect differences in speciation and extinction rates

From its beginnings, life on Earth has been marked by the rise and fall of groups of organisms. Anaerobic prokaryotes originated, flourished, and then declined as the oxygen content of the atmosphere rose. Billions of years later, the first tetrapods emerged from the sea, giving rise to several major new groups of organisms. One of these, the amphibians, went on to dominate life on land for 100 million years, until other tetrapods (including dinosaurs and, later, mammals) replaced them as the dominant terrestrial vertebrates.

▼ Figure 25.14 How speciation and extinction affect diversity. The species diversity of an evolutionary lineage will increase when more new member species originate than are lost to extinction. In this hypothetical phylogenetic tree, each horizontal branch represents one species. By 2 million years ago both lineage A and lineage B have given rise to four species, and no species have become extinct (denoted by a dagger symbol, †). By time 0, however, lineage A contains only one species, while lineage B contains eight species.



VISUAL SKILLS *Consider the period from 2 million years ago to time 0. For each lineage, determine how many speciation and extinction events occurred during that time.*

The rise and fall of these and other major groups of organisms have shaped the history of life. Narrowing our focus, we can also see that the rise or fall of any particular group is related to the speciation and extinction rates of its member species **(Figure 25.14)**. Just as a population increases in size when there are more births than deaths, the rise of a group of organisms occurs when more new species are produced than are lost to extinction. The reverse occurs when a group is in decline. In the **Scientific Skills Exercise**, you can interpret data from the fossil record about changes in a group of snail species in the early Paleogene period. Such changes in the fates of groups of organisms have been influenced by large-scale processes such as plate tectonics, mass extinctions, and adaptive radiations.

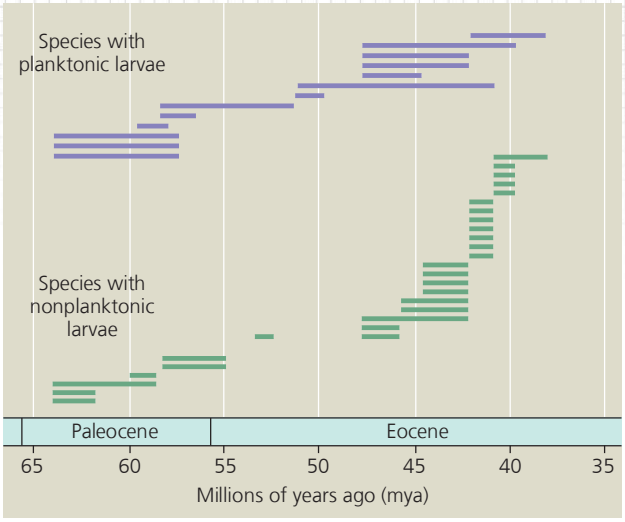
Scientific Skills Exercise

Estimating Quantitative Data from a Graph and Developing Hypotheses



Do Ecological Factors Affect Evolutionary Rates? Researchers studied the fossil record to investigate whether differing modes of larval dispersal might explain species longevity within one taxon of marine snails, the family Volutidae. Some of the snail species had nonplanktonic larvae: They developed directly into adults without a swimming stage. Other species had planktonic larvae: They had a swimming stage and could disperse very long distances. The adults of these planktonic species tended to have broad geographic distributions, whereas nonplanktonic species tended to be more isolated.

How the Research Was Done The researchers studied the stratigraphic distribution of volutes in outcrops of sedimentary rocks located along North America's Gulf coast. These rocks, which formed from 66 to 37 million years ago, early in the Paleogene period, are an excellent source of well-preserved snail fossils. The researchers were able to classify each fossil species of volute snail as having planktonic or nonplanktonic larvae based on features of the earliest formed whorls of the snail's shell. Each bar in the graph shows how long one species of snail persisted in the fossil record.



INTERPRET THE DATA

1. You can estimate quantitative data (fairly precisely) from a graph. The first step is to obtain a conversion factor by measuring along an axis that has a scale. In this case, 25 million years (my; from 60 to 35 million years ago [mya] on the *x*-axis) is represented by a distance of 7.0 cm. This yields a conversion factor (a ratio) of 25 my/7.0 cm = 3.6 my/cm. To estimate the time period represented by a horizontal bar on this graph, measure the length of that bar in centimeters and multiply that measurement by the conversion factor, 3.6 my/cm. For example, a bar that measures 1.1 cm on the graph represents a persistence time of 1.1 cm × 3.6 my/cm = 4 million years.
2. Calculate the mean (average) persistence times for species with planktonic larvae and species with nonplanktonic larvae.
3. Count the number of new species that form in each group beginning at 60 mya (the first three species in each group were present around 64 mya, the first time period sampled, so we don't know when those species first appear in the fossil record).
4. Propose a hypothesis to explain the differences in longevity of snail species with planktonic and nonplanktonic larvae.

Data from T. A. Hansen, Larval dispersal and species longevity in Lower Tertiary gastropods, *Science* 199:885–887 (1978). Reprinted with permission from AAAS.

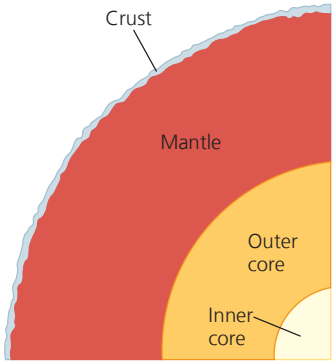
Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

Plate Tectonics

If photographs of Earth were taken from space every 10,000 years and spliced together to make a movie, it would show something many of us find hard to imagine: The seemingly "rock solid" continents we live on move over time. Over the past billion years, there have been three occasions (1 billion, 600 million, and 250 million years ago) when most of the landmasses of Earth came together to form a supercontinent, then later broke apart. Each time, this breakup yielded a different configuration of continents. Based on the directions in which the continents are moving today, some geologists have estimated that a new supercontinent will form roughly 250 million years from now.

According to the theory of **plate tectonics**, the continents are part of great plates of Earth's crust that essentially float on the hot, underlying portion of the mantle **(Figure 25.15)**. Movements in the mantle cause the plates to move over time in a process called *continental drift*. Geologists can measure the rate at which the plates are moving now, usually only a few centimeters per year. They can also infer the past locations of the continents using the magnetic signal recorded in rocks at the time of their formation. This method works because as a continent shifts its position over time, the direction of magnetic north recorded in its newly formed rocks also changes.

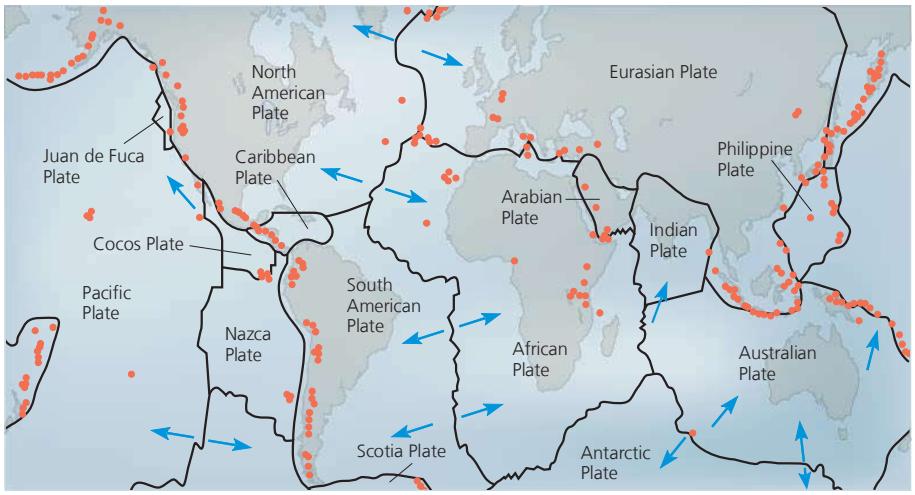
▼ Figure 25.15 Cutaway view of Earth. The thickness of the crust is exaggerated here.



Earth's major tectonic plates are shown in **Figure 25.16**. Many important geologic processes, including the formation of mountains and islands, occur at plate boundaries. In some cases, two plates are moving away from each other, as are the North American and Eurasian plates, which

are currently drifting apart at a rate of about 2 cm per year. In other cases, two plates are sliding past each other, forming regions where earthquakes are common. California's infamous San Andreas Fault is part of a border where two plates slide past each other. In still other cases, two plates collide, producing violent upheavals and forming new mountains along the plate boundaries. One spectacular example of this occurred 45 million years ago, when the Indian plate crashed into the Eurasian plate, starting the formation of the Himalayan mountains.

▼ Figure 25.16 Earth's major tectonic plates. The blue arrows indicate direction of movement. The reddish orange dots represent zones of violent tectonic activity.



Mastering Biology **HHMI Animation: Plate Tectonics** hhmi BioInteractive

Consequences of Continental Drift

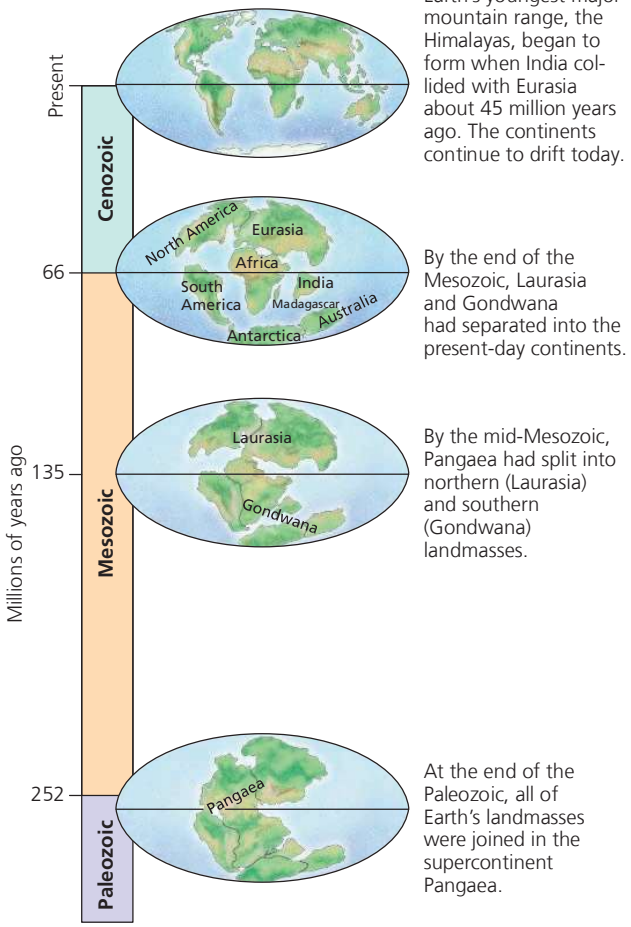
Plate movements rearrange geography slowly, but their cumulative effects are dramatic. In addition to reshaping the physical features of our planet, continental drift also has a major impact on life on Earth.

One reason for this is that continental drift alters the habitats in which organisms live. Consider the changes shown in **Figure 25.17**. About 250 million years ago, plate movements brought previously separated landmasses together into a supercontinent named **Pangaea**. Ocean basins became deeper, which drained shallow coastal seas. At that time, as now, most marine species inhabited shallow waters, and the formation of Pangaea destroyed much of that habitat. Pangaea's interior was cold and dry, probably an even more severe environment than that of central Asia today. Overall, the formation of Pangaea greatly altered the physical environment and climate, which drove some species to extinction and provided new opportunities for groups of organisms that survived the crisis.

Organisms are also affected by the climate change that results when a continent shifts its location. The southern tip of Labrador, Canada, for example, once was located in the tropics but has moved 40° to the north over the last 200 million years. When faced with the changes in climate that such shifts in position entail, organisms adapt, move to a new location, or become extinct (this last outcome occurred for many organisms stranded on Antarctica, which separated from Australia 40 million years ago).

Continental drift also promotes allopatric speciation on a grand scale. When supercontinents break apart, regions that once were connected become isolated. As the continents drifted apart over the last 200 million years, each became a separate evolutionary arena, with lineages of plants and animals that diverged from those on other continents. For example, marsupial mammals fill ecological roles in Australia analogous to those filled by eutherians (placental mammals) on other continents (see Figure 22.18). Fossil evidence shows

▼ Figure 25.17 The history of continental drift during the Phanerozoic eon.



VISUAL SKILLS *Is the Australian plate's current direction of movement (see Figure 25.16) similar to the direction it traveled over the past 66 million years?*

that marsupial mammals originated in what is now Asia and reached Australia via South America and Antarctica while the continents were still joined. The subsequent breakup of the southern continents set Australia "afloat," like a giant raft of marsupials. In Australia, marsupials diversified, and the few eutherians (placental mammals) that lived there became extinct; on other continents, most marsupials became extinct and the eutherians diversified.

Finally, continental drift can help explain puzzling geographic distributions of extinct organisms, such as fossils of the same species of Permian freshwater reptiles found in both Brazil and the West African nation of Ghana. These two parts of the world, now separated by 3,000 km of ocean, were joined together when these reptiles were living.

Mastering Biology **HHMI Video: Animated Life: Pangea, Wegener, and Continental Drift**

Mass Extinctions

The fossil record shows that the overwhelming majority of species that ever lived are now extinct. A species may become extinct for many reasons. Its habitat may have been destroyed, or its environment may have changed in a manner unfavorable to the species. For example, if ocean temperatures fall by even a few degrees, species that are otherwise well adapted may perish. Even if physical factors in the environment remain stable, biological factors may change—the origin of one species can spell doom for another.

Although extinction occurs regularly, at certain times disruptive changes to the global environment have caused the rate of extinction to increase dramatically. The result is a **mass extinction**, in which large numbers of species become extinct worldwide.

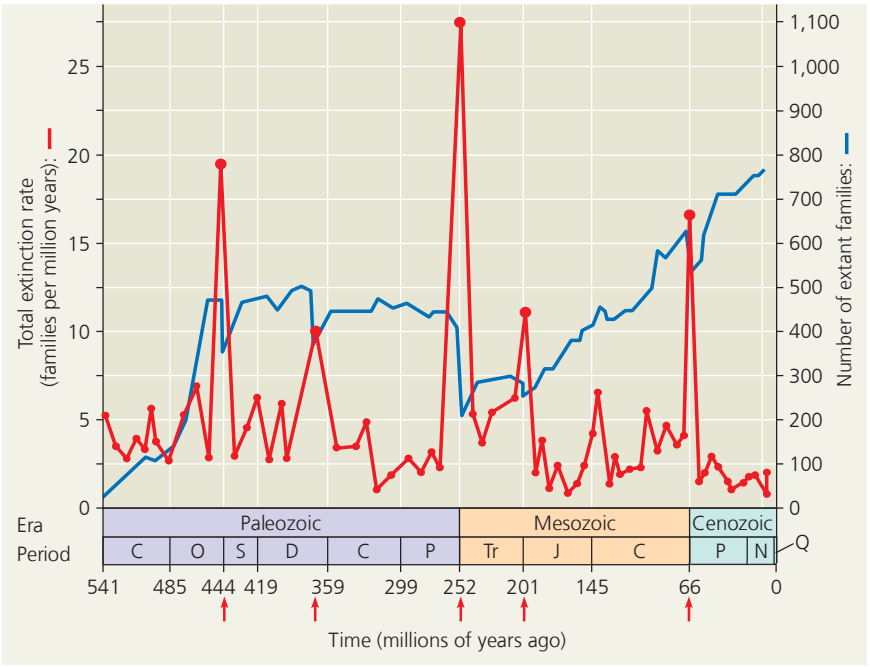
The "Big Five" Mass Extinction Events

Five mass extinctions are documented in the fossil record over the past 500 million years **(Figure 25.18)**. These events are particularly well documented for the decimation of hard-bodied animals that lived in shallow seas, the organisms for which the fossil record is most complete. In each mass extinction, 50% or more of marine species became extinct.

Two mass extinctions—the Permian and the Cretaceous—have received the most attention. The Permian mass extinction, which defines the boundary between the Paleozoic and Mesozoic eras (252 million years ago), claimed about 96% of marine animal species and drastically altered life in the ocean. Terrestrial life was also affected. For example, 8 out of 27 known orders of insects were wiped out. This mass extinction occurred in less than 500,000 years, possibly in just a few thousand years—an instant in the context of geologic time.

The Permian mass extinction occurred during the most extreme episode of volcanism in the past 500 million years. Geologic data indicate that 1.6 million km^2 (roughly half the size of Western Europe) in Siberia was covered with lava hundreds of meters thick. The eruptions are thought to have produced enough carbon dioxide to warm the global climate by an estimated 6°C, harming many temperature-sensitive species. The rise in atmospheric CO_2 levels would also have led to ocean acidification, thereby reducing the availability of calcium carbonate, which is required by reef-building corals and many shell-building species (see Figure 3.12). The eruptions would also have added nutrients such as phosphorus to marine ecosystems, stimulating the growth of microorganisms. Upon their deaths, these microorganisms would have provided food for bacterial decomposers. Bacteria use oxygen as they decompose the bodies of dead organisms, thus causing oxygen concentrations to drop. This would have harmed oxygen-breathers and promoted the growth of anaerobic bacteria that emit a poisonous metabolic by-product, hydrogen sulfide (H_2S) gas. Overall, the volcanic eruptions may have triggered a series of catastrophic events that together resulted in the Permian mass extinction.

▼ Figure 25.18 Mass extinction and the diversity of life. The five generally recognized mass extinction events, indicated by red arrows, represent peaks in the extinction rate of marine animal families (red line and left vertical axis). These mass extinctions interrupted the overall increase, over time, in the number of extant families of marine animals (blue line and right vertical axis).



INTERPRET THE DATA *As mentioned in the text, 96% of marine animal species became extinct in the Permian mass extinction (252 million years ago). Explain why the blue curve shows only a 50% drop at that time.*

The Cretaceous mass extinction occurred 66 million years ago. This event extinguished more than half of all marine species and eliminated many families of terrestrial plants and animals, including all dinosaurs (except birds, which are members of the same group; see Figure 34.25). One clue to a possible cause of the Cretaceous mass extinction is a thin layer of clay enriched in iridium that dates to the time of the mass extinction. Iridium is an element that is very rare on Earth but common in many of the meteorites and other extraterrestrial objects that occasionally fall to Earth. As a result, researchers proposed that this clay is fallout from a huge cloud of debris that billowed into the atmosphere when an asteroid collided with Earth. This cloud would have blocked sunlight and caused a sudden drop in global temperatures lasting for several months to years.

Is there evidence of such an asteroid? Research has focused on the Chicxulub crater, a 66-million-year-old scar beneath sediments off the coast of Mexico **(Figure 25.19)**. The crater is the right size to have been caused by an object with a diameter of 10 km. When the impact occurred, many species may have been particularly vulnerable to extinction because recent large-scale volcanic eruptions had already caused their populations to decline. Moreover, a 2018 study estimated that wildfires resulting from the impact contributed to a sharp rise in atmospheric CO_2 levels, causing a period of global warming that lasted 100,000 years—yet another stress for populations already in decline. Critical evaluation of these and other hypotheses for mass extinctions continues.

▼ Figure 25.19 A trauma for Cretaceous life. Beneath the Caribbean Sea, the 66-million-year-old Chicxulub crater measures 180 km across. The horseshoe shape of the crater and the pattern of debris in sedimentary rocks indicate that an asteroid struck at a low angle. This drawing represents the impact and its immediate effect: a cloud of hot vapor and debris that could have killed many of the plants and animals in North America within hours and ignited massive wildfires.



Mastering Biology **HHMI Video: The Day the Mesozoic Died**

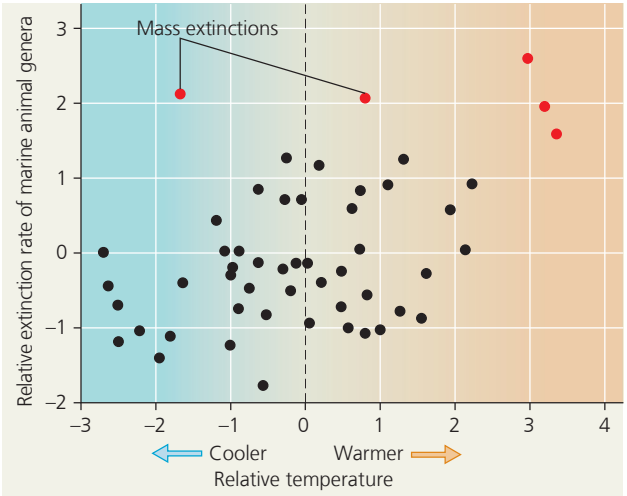
Is a Sixth Mass Extinction Under Way?

As you will read further in Concept 56.1, human actions, such as habitat destruction, are modifying the global environment to such an extent that many species are threatened with extinction. More than 1,000 species have become extinct in the last 400 years. Scientists estimate that this rate is 100 to 1,000 times the typical background rate seen in the fossil record. Is a sixth mass extinction now in progress?

This question is difficult to answer, in part because it is hard to document the total number of extinctions occurring today. Tropical rain forests, for example, harbor many undiscovered species. As a result, destroying tropical forest may drive species to extinction before we even learn of them.

Such uncertainties make it hard to assess the full extent of the current extinction crisis. Even so, it is clear that losses to date have not reached those of the "big five" mass extinctions, in which large percentages of Earth's species became extinct. This does not in any way discount the seriousness of today's situation. Monitoring programs show that many species are declining at an alarming rate due to habitat loss, introduced species, overharvesting, and other factors. Recent studies on a variety of organisms, including lizards, pine trees, and polar bears, suggest that climate change may hasten some of these declines. The fossil record also highlights the potential importance of climate change: Over the last 500 million years, extinction rates have tended to increase when global temperatures were high **(Figure 25.20)**.

▼ Figure 25.20 Fossil extinctions and temperature. Extinction rates increased when global temperatures were high. Temperatures were estimated using ratios of oxygen isotopes and converted to an index in which 0 is the overall average temperature.



Overall, the evidence suggests that unless dramatic actions are taken, a sixth, human-caused mass extinction is likely to occur within the next few centuries.

Consequences of Mass Extinctions

Mass extinctions have significant and long-term effects. By eliminating large numbers of species, a mass extinction can reduce a thriving and complex ecological community to a pale shadow of its former self. And once an evolutionary lineage disappears, it cannot reappear. The course of evolution is changed forever. Consider what would have happened if the early primates living 66 million years ago had died out in the Cretaceous mass extinction. Humans would not exist, and life on Earth would differ greatly from what it is today.

The fossil record shows that it typically takes 5–10 million years for the diversity of life to recover to previous levels after a mass extinction. In some cases, it has taken much longer than that: It took about 100 million years for the number of marine families to recover after the Permian mass extinction (see Figure 25.18). These data have sobering implications. If current trends continue and a sixth mass extinction occurs, it will take millions of years for life on Earth to recover.

Mass extinctions can also alter ecological communities by changing the types of organisms residing there. For example, after the Permian and Cretaceous mass extinctions, the percentage of marine organisms that were predators increased substantially **(Figure 25.21)**. A rise in the number of predators can increase both the risks faced by prey and the competition among predators for food. In addition, mass extinctions can curtail lineages with novel and advantageous features. For example, in the late Triassic period, a group of gastropods (snails and their relatives) arose that could drill through the shells of bivalves (such as clams) and feed on the animals inside. Although shell drilling provided access to a new and abundant source of food, this newly formed group was wiped out during the mass extinction at the end of the Triassic (about 200 million years ago). Another 120 million years passed before another group of gastropods (the oyster drills) exhibited the ability to drill through shells. As their predecessors might have done if they had not originated at an unfortunate time, oyster drills have since diversified into many new species. Finally, by eliminating so many species, mass extinctions can pave the way for adaptive radiations, in which new groups of organisms proliferate.

Adaptive Radiations

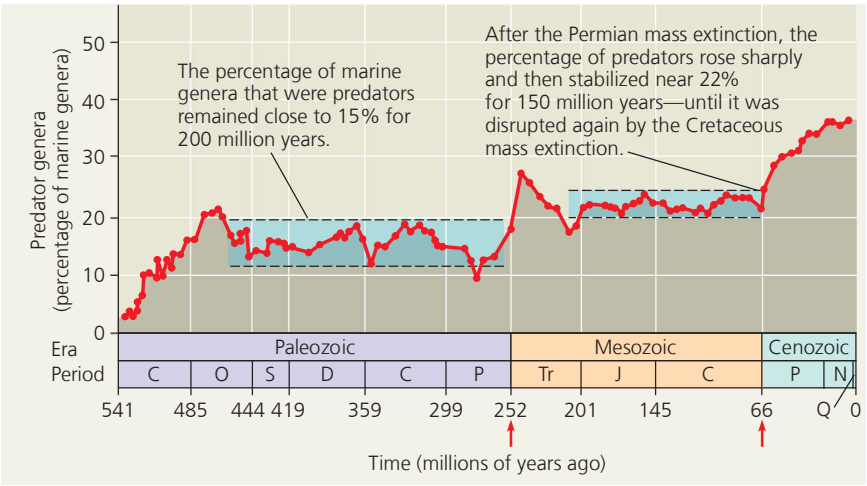
The fossil record shows that the diversity of life has increased over the past 250 million years (see blue line in Figure 25.18). This increase has been fueled by **adaptive radiations**, periods of evolutionary change in which groups of organisms form many new species whose adaptations allow them to fill different ecological roles, or niches, in their communities. Large-scale adaptive radiations occurred after each of the big five mass extinctions, when survivors became adapted to the many vacant ecological niches. Adaptive radiations have also occurred in groups of organisms that possessed major evolutionary innovations, such as seeds or armored body coverings, or that colonized regions in which they faced little competition from other species.

Worldwide Adaptive Radiations

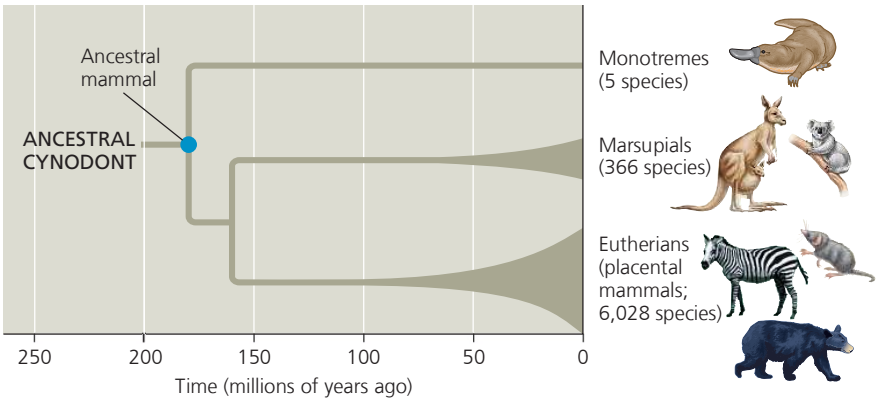
Fossil evidence indicates that mammals underwent a dramatic adaptive radiation after the extinction of terrestrial dinosaurs 66 million years ago **(Figure 25.22)**. Although mammals originated about 180 million years ago, the mammal fossils older than 66 million years are mostly small and show less morphological diversity than found today. Many species appear to have been nocturnal based on their large eye sockets, similar to those in living nocturnal mammals. A few early mammals were intermediate in size, such as *Repenomamus giganticus*, a 1-m-long predator that lived 130 million years ago—but none approached the size of many dinosaurs. Early mammals may have been restricted in size and diversity because they were eaten or outcompeted by the larger and more diverse dinosaurs. With the disappearance of the dinosaurs (except for birds), mammals expanded greatly in both diversity and size, filling the ecological roles once occupied by terrestrial dinosaurs.

The history of life has also been greatly altered by radiations in which groups of organisms increased in diversity as they came to play entirely new ecological roles in their communities. As we'll explore in later chapters, examples include the rise of photosynthetic prokaryotes, the evolution

▼ Figure 25.21 Mass extinctions and ecology. The Permian and Cretaceous mass extinctions (indicated by red arrows) altered the ecology of the oceans by increasing the percentage of marine genera that were predators.



▼ Figure 25.22 Adaptive radiation of mammals.

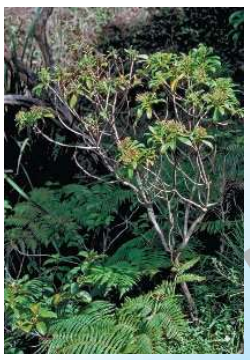


of large predators in the Cambrian explosion, and the radiations following the colonization of land by plants, insects, and tetrapods. Each of these last three radiations was associated with major evolutionary innovations that facilitated life on land. The radiation of plants, for example, was associated with key adaptations, such as stems that support plants against gravity and a waxy coat that protects leaves from water loss. Finally, organisms that arise in an adaptive radiation can serve as a new source of food for still other organisms. In fact, the diversification of plants stimulated a series of adaptive radiations in insects that ate or pollinated plants, one reason that insects are the most diverse group of animals on Earth today.

Regional Adaptive Radiations

Striking adaptive radiations have also occurred over more limited geographic areas. Such radiations can be initiated when a few organisms make their way to a new, often distant location in which they face relatively little competition from other organisms. The Hawaiian archipelago is one of the world's great showcases of this type of adaptive radiation **(Figure 25.23)**.

▼ Figure 25.23 Adaptive radiation on the Hawaiian Islands. Molecular analysis indicates that these remarkably varied Hawaiian plants, known collectively as the "silversword alliance," are all descended from an ancestral tarweed that arrived on the islands from North America about 5 million years ago. Silverswords have since spread into different habitats and formed new species with strikingly different adaptations.



Dubautia laxa



Close North American relative, the tarweed *Carlquistia muirii*



Argyroxiphium sandwicense



Dubautia waialealae



Dubautia scabra



Dubautia linearis

Mastering Biology
Animation: Overview of Macroevolution

Located about 3,500 km from the nearest continent, the volcanic islands are progressively older as one follows the chain toward the northwest; the youngest island, Hawaii, is less than a million years old and still has active volcanoes. Each island was born "naked" and was gradually populated by stray organisms that rode the ocean currents and winds either from far-distant land areas or from older islands of the archipelago itself. The physical diversity of each island, including immense variation in soil conditions, elevation, and rainfall, provides many opportunities for evolutionary divergence by natural selection. Multiple invasions followed by speciation events have ignited an explosion of adaptive radiation in Hawaii. As a result, thousands of species that inhabit the islands are found nowhere else on Earth. Among plants, for example, about 1,100 species are unique to the Hawaiian Islands. Unfortunately, many of these species are now facing an elevated risk of extinction due to human actions such as habitat destruction and the introduction of non-native plant species.

CONCEPT CHECK 25.4

1. Explain the consequences of plate tectonics for life on Earth.
2. What factors promote adaptive radiations?
3. **WHAT IF?** Based on evidence from previous mass extinctions, describe ecological and evolutionary consequences that could result if a sixth human-caused mass extinction occurs.

For suggested answers, see Appendix A.

CONCEPT 25.5

Major changes in body form can result from changes in the sequences and regulation of developmental genes

The fossil record tells us what the great changes in the history of life have been and when they occurred. Moreover, an understanding of plate tectonics, mass extinction, and adaptive radiation provides a picture of how those changes came about. But we can also seek to understand the intrinsic biological mechanisms that underlie changes seen in the fossil record. For this, we turn to genetic mechanisms of change, paying particular attention to genes that influence development.

Effects of Developmental Genes

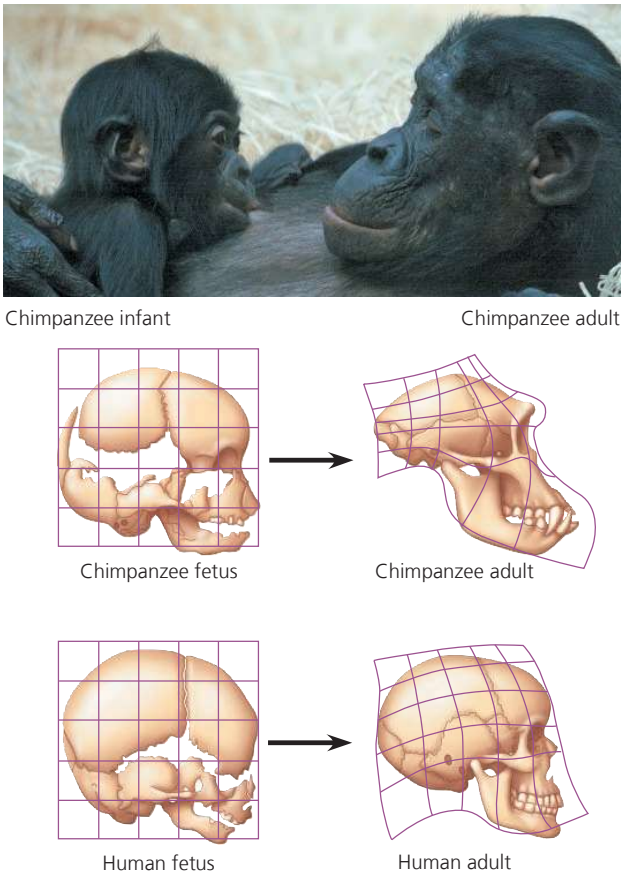
As you read in Concept 21.6, "evo-devo"—research at the interface between evolutionary biology and developmental biology—is illuminating how slight genetic differences can produce major morphological differences between species. In particular, large morphological differences can result from genes that alter the rate, timing, and spatial pattern of change in an organism's form as it develops from a zygote into an adult.

Changes in Rate and Timing

Many striking evolutionary transformations are the result of **heterochrony** (from the Greek *hetero*, different, and *chronos*, time), an evolutionary change in the rate or timing of developmental events. For example, an organism's shape depends in part on the relative growth rates of different body parts during development. Changes to these rates can alter the adult form substantially, as seen in the contrasting shapes of human and chimpanzee skulls **(Figure 25.24)**. Other examples of the dramatic evolutionary effects of heterochrony include how increased growth rates of finger bones yielded the skeletal structure of wings in bats (see Figure 22.15) and how slowed growth of leg and pelvic bones led to the reduction and eventual loss of hind limbs in whales (see Figure 22.20).

Heterochrony can also alter the timing of reproductive development relative to the development of nonreproductive organs. If the development of reproductive organs accelerates compared to that of other organs, the sexually mature stage of a species may retain body features that were juvenile structures in an ancestral species, a condition called

▼ Figure 25.24 Relative skull growth rates. In the human evolutionary lineage, mutations slowed the growth of the jaw relative to other parts of the skull. As a result, in humans the skull of an adult is more similar to the skull of an infant than is the case for chimpanzees.





▲ **Figure 25.25 Paedomorphosis.** The adults of some species retain features that were juvenile in ancestors. This salamander is an axolotl, an aquatic species becomes a sexually mature adult while retaining certain larval (tadpole) characteristics, including gills.

paedomorphosis (from the Greek *paedos*, of a child, and *morphosis*, formation). For example, most salamander species have aquatic larvae that undergo metamorphosis in becoming adults. But some species grow to adult size and become sexually mature while retaining gills and other larval features **(Figure 25.25)**. Such an evolutionary alteration of developmental timing can produce animals that appear very different from their ancestors, even though the overall genetic change may be small. Indeed, recent evidence indicates that a change at a single locus was probably sufficient to bring about paedomorphosis in the axolotl salamander, although other genes may have contributed as well.

Changes in Spatial Pattern

Substantial evolutionary changes can also result from alterations in genes that control the spatial organization of body parts. For example, master regulatory genes called **homeotic genes** (see Concept 18.4) determine such basic features as where a pair of wings and legs will develop on a bird or how a plant's flower parts are arranged.

The products of one class of homeotic genes, the *Hox* genes, provide positional information in an animal embryo. This information prompts cells to develop into structures appropriate for a particular location. Changes in *Hox* genes or in how they are expressed can have a profound impact on morphology. For example, among crustaceans, a change in the location where two *Hox* genes (*Ubx* and *Scr*) are expressed correlates with the conversion of a swimming appendage to a feeding appendage. Similarly, when comparing plant species, changes to the expression of homeotic genes known as *MADS-box* genes can produce flowers that differ dramatically in form (see Concept 35.5).

The Evolution of Development

The 560-million-year-old fossils of Ediacaran animals (see Figure 25.11) suggest that a set of genes sufficient to produce complex animals existed at least 25 million years *before* the Cambrian explosion. If such genes have existed for so long, how can we explain the astonishing increases in diversity seen during and since the Cambrian explosion?

Adaptive evolution by natural selection provides one answer to this question. As we've seen throughout this unit, by sorting among differences in the sequences of protein-encoding genes, selection can improve adaptations rapidly. In addition, new genes (created by gene duplication events) can take on new metabolic and structural functions, as can existing genes that are regulated in new ways.

Examples in the previous section suggest that developmental genes may have been particularly important. Thus, we'll turn next to how new morphological forms can arise from changes in the nucleotide sequences or regulation of developmental genes.

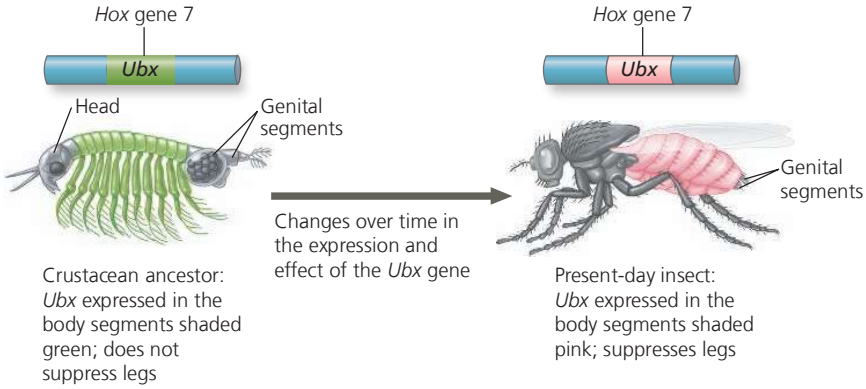
Changes in Gene Sequence

New developmental genes arising after gene duplication events probably facilitated the origin of novel morphological forms. But since other genetic changes also may have occurred at such times, it can be difficult to establish causal links between genetic and morphological changes that occurred in the past.

This difficulty was sidestepped in a study of developmental changes associated with the divergence of six-legged insects from crustacean ancestors that had more than six legs. (As discussed in Concept 33.4, insects arose from within a subgroup of the crustaceans, the traditional name for organisms such as shrimp, crabs, and lobsters.) Crustaceans and insects differ in the pattern of expression and the effects of the *Hox* gene *Ubx*: In particular, in insects, *Ubx* suppresses leg formation where it is expressed **(Figure 25.26)**.

To examine the workings of this gene, researchers cloned the *Ubx* gene from an insect, the fruit fly *Drosophila*, and from

▼ **Figure 25.26 Effects of the *Hox* gene *Ubx* on the insect body plan.** In crustaceans, the *Hox* gene *Ubx* is expressed in the region shaded green, the body segments between the head and genital segments. In insects, *Ubx* is expressed in only a subset (shaded pink) of the homologous body segments, where it suppresses leg formation.



a crustacean, the brine shrimp *Artemia*. Next, they genetically engineered fruit fly embryos to express either the *Drosophila Ubx* gene or the *Artemia Ubx* gene throughout their bodies. The *Drosophila* gene suppressed 100% of the limbs in the embryos, as expected, whereas the *Artemia* gene suppressed only 15%.

The researchers then sought to uncover key steps involved in the evolutionary transition from an ancestral *Ubx* gene to an insect *Ubx* gene. Their approach was to identify mutations that would cause the *Artemia Ubx* gene to suppress leg formation, thus making its gene act more like an insect *Ubx* gene. To do this, they constructed a series of "hybrid" *Ubx* genes, each of which contained known segments of the *Drosophila Ubx* gene and known segments of the *Artemia Ubx* gene. By inserting these hybrid genes into fruit fly embryos (one hybrid gene per embryo) and observing their effects on leg development, the researchers were able to pinpoint the exact amino acid changes responsible for the suppression of additional limbs in insects. In so doing, this study provided evidence that particular changes in the nucleotide sequence of a developmental gene contributed to a major evolutionary change: the origin of the six-legged insect body plan.

Changes in Gene Regulation

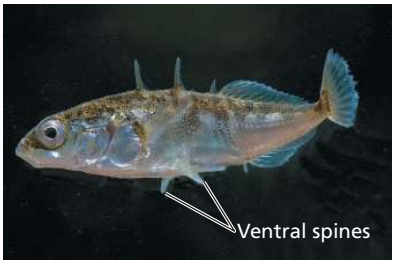
A change in the nucleotide sequence of a gene may affect its function wherever the gene is expressed, while changes in the regulation of gene expression can be limited to one cell type (see Concept 18.4). Thus, a change in the regulation of a developmental gene may have fewer harmful side effects than a change to the sequence of the gene. This reasoning has prompted researchers to suggest that changes in the form of organisms may often be caused by mutations that affect the regulation of developmental genes—not their sequences.

This idea is supported by studies of a variety of species, including threespine stickleback fish. These fish live in the open ocean and in shallow, coastal waters. In western Canada, they also live in lakes formed when the coastline receded during the past 12,000 years.

▼ Figure 25.27 Inquiry

What causes the loss of spines in lake stickleback fish?

Experiment Marine populations of the threespine stickleback fish (*Gasterosteus aculeatus*) have a set of protective spines on their lower (ventral) surface; however, these spines have been lost or reduced in some lake populations of this fish. Researchers performed genetic crosses and found that most of the reduction in spine size resulted from the effects of a single developmental gene, *Pitx1*. The researchers then tested two hypotheses about how *Pitx1* causes this morphological change.



▲ **Threespine stickleback (*Gasterosteus aculeatus*)**

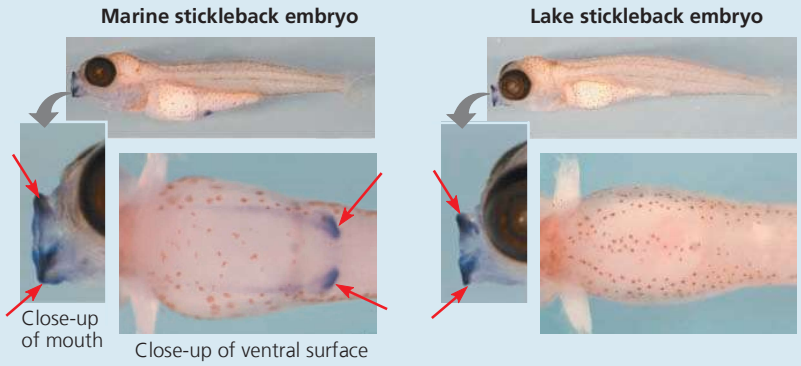
Hypothesis A: A change in the DNA sequence of *Pitx1* had caused spine reduction in lake populations. To test this idea, the team used DNA sequencing to compare the coding sequence of the *Pitx1* gene between marine and lake stickleback populations.

Hypothesis B: A change in the regulation of the expression of *Pitx1* had caused spine reduction. To test this idea, the researchers monitored where in the developing embryo the *Pitx1* gene was expressed. They conducted whole-body *in situ* hybridization experiments (see Concept 20.2) using *Pitx1* DNA as a probe to detect *Pitx1* mRNA in the fish.

Results

Test of Hypothesis A: Are there differences in the coding sequence of the *Pitx1* gene in marine and lake stickleback fish? → **Result: No** → The 283 amino acids of the *Pitx1* protein are identical in marine and lake stickleback populations.

Test of Hypothesis B: Are there any differences in the regulation of expression of *Pitx1?* → **Result: Yes** → Red arrows (→) indicate regions of *Pitx1* gene expression in the photographs below. *Pitx1* is expressed in the ventral spine and mouth regions of developing marine stickleback fish but only in the mouth region of developing lake stickleback fish.



Conclusion The loss or reduction of ventral spines in lake populations of threespine stickleback fish appears to have resulted primarily from a change in the regulation of *Pitx1* gene expression, not from a change in the gene's sequence.

Data from M. D. Shapiro et al., Genetic and developmental basis of evolutionary pelvic reduction in threespine sticklebacks, *Nature* 428:717–723 (2004).

WHAT IF? *Describe the set of results that would have led researchers to the conclusion that a change in the coding sequence of the* Pitx1 *gene was more important than a change in regulation of gene expression.*

Marine stickleback fish have a pair of spines on their ventral (lower) surface, which deter some predators. These spines are often reduced or absent in stickleback fish living in lakes that lack predatory fishes and that are also low in calcium. Spines may have been lost in such lakes because they are not advantageous in the absence of predators, and the limited calcium is needed for purposes other than constructing spines.

At the genetic level, the developmental gene *Pitx1* was known to influence whether stickleback fish have ventral spines. Was the reduction of spines in some lake populations due to changes in the *Pitx1* gene or to changes in how the gene is expressed **(Figure 25.27)**? The researchers' results indicate that the regulation of gene expression has changed, not the DNA sequence. Moreover, lake stickleback fish do express the *Pitx1* gene in tissues not related to the production of spines (for example, the mouth), illustrating how morphological change can be caused by altering the expression of a developmental gene in some parts of the body but not others. In a follow-up study, researchers showed that changes to the *Pel* enhancer, a noncoding DNA region that affects expression of the *Pitx1* gene, resulted in the reduction of ventral spines in lake sticklebacks. Overall, results from studies on stickleback fish provide a clear and detailed example of how changes in gene regulation can alter the form of individual organisms and ultimately lead to evolutionary change in populations.

Mastering Biology **HHMI Video: The Making of the Fittest: Evolving Switches, Evolving Bodies (Stickleback)**



Mastering Biology **Interview with Cassandra Extavour: Studying the evolution of genes that control development (see the interview before Chapter 22)**

CONCEPT CHECK 25.5

1. Explain how new body forms can originate by heterochrony.
2. Why is it likely that *Hox* genes have played a major role in the evolution of novel morphological forms?
3. **MAKE CONNECTIONS** Given that changes in morphology are often caused by changes in the regulation of gene expression, predict whether noncoding DNA is likely to be affected by natural selection. (Review Concept 18.3.)

For suggested answers, see Appendix A.

CONCEPT 25.6

Evolution is not goal oriented

What does our study of macroevolution tell us about how evolution works? One lesson is that throughout the history of life, the origin of new species has been affected by both the small-scale factors described in Concept 23.3 (such as natural selection operating in populations) and the large-scale factors described in this chapter (such as continental drift promoting bursts of speciation throughout the globe).

Moreover, to paraphrase the Nobel Prize–winning geneticist François Jacob, evolution is like tinkering—a process in which new forms arise by the modification of existing structures or existing developmental genes. Over time, such tinkering has led to the three key features of the natural world described on the opening page of Chapter 22: the striking ways in which organisms are suited for life in their environments, the many shared characteristics of life, and the rich diversity of life.

Evolutionary Novelties

François Jacob's view of evolution harkens back to Darwin's concept of descent with modification. As new species form, novel and complex structures can arise as gradual modifications of ancestral structures. In many cases, complex structures have evolved in increments from simpler versions that performed the same basic function. For example, consider the human eye, an intricate organ constructed from numerous parts that work together in forming an image and transmitting it to the brain. How could the human eye have evolved in gradual increments? Some argue that if the eye needs all of its components to function, a partial eye could not have been of use to our ancestors.

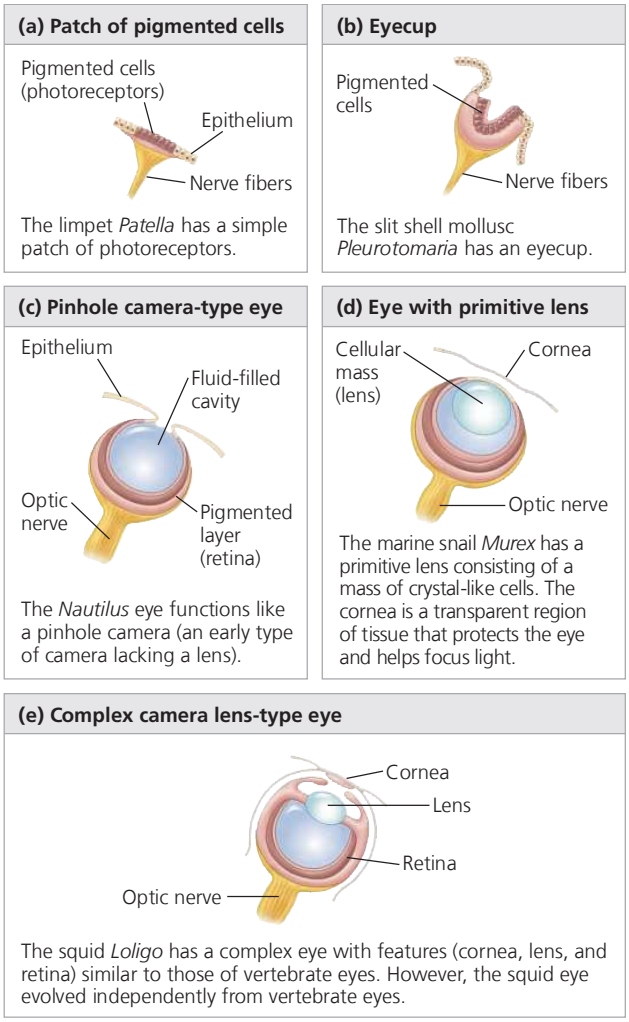
The flaw in this argument, as Darwin himself noted, lies in the assumption that only complicated eyes are useful. In fact, many animals depend on eyes that are far less complex than our own. The simplest eyes that we know of are patches of light-sensitive photoreceptor cells. These simple eyes appear to have had a single evolutionary origin and are now found in a variety of animals, including small molluscs called limpets. Such eyes have no equipment for focusing images, but they do enable the animal to distinguish light from dark. Limpets cling more tightly to their rock when a shadow falls on them, a behavioral adaptation that reduces the risk of being eaten **(Figure 25.28)**. Limpets have had a long evolutionary history, demonstrating that their "simple" eyes are quite adequate to support their survival and reproduction.

In the animal kingdom, complex eyes have evolved independently from such basic structures many times. Some

▼ Figure 25.28 **Limpets (*Patella vulgata*), molluscs that can sense light and dark with a simple patch of photoreceptor cells.**



▼ Figure 25.29 A range of eye complexity among molluscs.



Mastering Biology BBC Video: How Did Eyes Evolve?

molluscs, such as squids and octopuses, have eyes as complex as those of humans and other vertebrates **(Figure 25.29)**. Although complex mollusc eyes evolved independently of vertebrate eyes, both evolved from a simple cluster of photoreceptor cells present in a common ancestor. In each case, the complex eye evolved through a series of steps that benefited the eyes' owners at every stage. Evidence of their independent evolution can be found in their structure: Vertebrate eyes detect light at the back layer of the retina and conduct nerve impulses toward the front, while complex mollusc eyes do the reverse.

Throughout their evolutionary history, eyes retained their basic function of vision. But evolutionary novelties can also arise when structures that originally played one role gradually acquire a different one. For example, as cynodonts gave rise to early mammals, bones that formerly comprised the jaw hinge (the articular and quadrate; see Figure 25.7) were incorporated into the ear region of mammals, where they eventually took on a new function: the transmission of sound (see Concept 34.6). Structures that evolve in one context but become co-opted for another function are sometimes called *exaptations* to distinguish them from the adaptive origin of the original structure. Note that the concept of exaptation does not imply that a structure somehow evolves in anticipation of future use. Natural selection cannot predict the future; it can only improve a structure in the context of its *current* utility. Novel features, such as the new jaw hinge and ear bones of early mammals, can arise gradually via a series of intermediate stages, each of which has some function in the organism's current context.

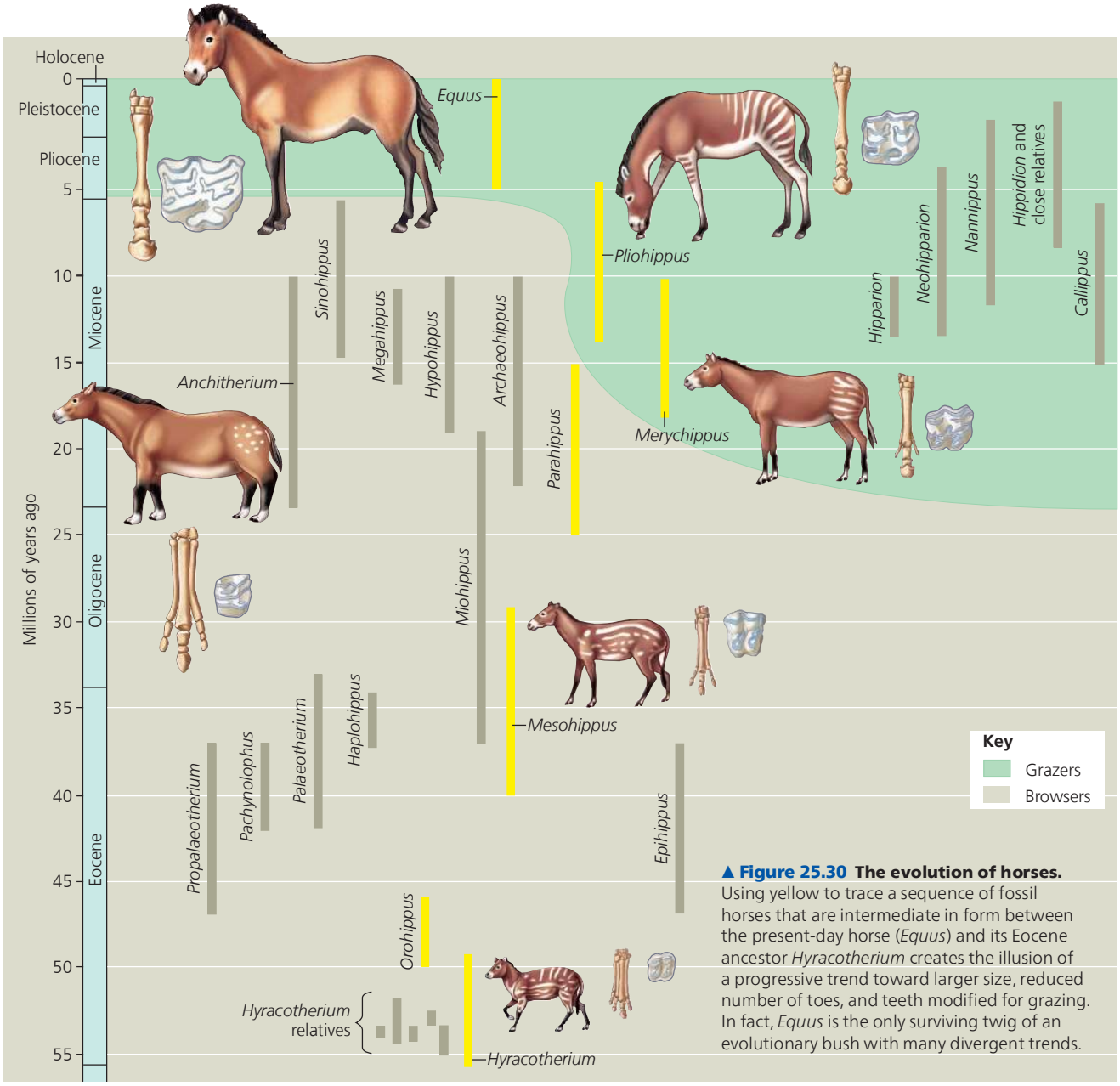
Mastering Biology HHMI Video: The Origin of Flight: What Use Is Half a Wing?

Evolutionary Trends

What else can we learn from patterns of macroevolution? Consider evolutionary "trends" observed in the fossil record. For instance, some evolutionary lineages exhibit a trend toward larger or smaller body size. An example is the evolution of the present-day horse (genus *Equus*), a descendant of the 55-million-year-old *Hyracotherium* **(Figure 25.30)**. About the size of a large dog, *Hyracotherium* had four toes on its front feet, three toes on its hind feet, and teeth adapted for browsing on bushes and trees. In comparison, present-day horses are larger, have only one toe on each foot, and possess teeth modified for grazing on grasses.

Extracting a single evolutionary progression from the fossil record can be misleading, however; it is like describing a bush as growing toward a single point by tracing only the branches that lead to that twig. For example, by selecting certain species from the available fossils, it is possible to arrange a succession of animals intermediate between *Hyracotherium* and living horses that shows a trend toward large, single-toed species (follow the yellow highlighting in Figure 25.30). However, if we consider *all* fossil horses known today, this apparent trend vanishes. The genus *Equus* did not evolve in a straight line; it is the only surviving twig of an evolutionary tree that is so branched that it is more like a bush. *Equus* actually descended through a series of speciation episodes that included several adaptive radiations, not all of which led to large, one-toed, grazing horses. In fact, phylogenetic analyses suggest that all lineages that include grazers are closely related to *Parahippus*; the many other horse lineages, all of which are now extinct, remained multi-toed browsers for 35 million years.

Branching evolution *can* result in a real evolutionary trend even if some species counter the trend. One model of long-term trends views species as analogous to individuals: Speciation is their birth, extinction is their death, and new species that diverge from them are their offspring. In this model, just as populations of individual organisms undergo natural selection, species undergo *species selection*. The species that endure the longest and generate the most new offspring species determine the direction of major evolutionary trends. The species selection model suggests that "differential speciation success" plays a role in macroevolution similar to the role of differential reproductive success



▲ Figure 25.30 The evolution of horses. Using yellow to trace a sequence of fossil horses that are intermediate in form between the present-day horse (*Equus*) and its Eocene ancestor *Hyracotherium* creates the illusion of a progressive trend toward larger size, reduced number of toes, and teeth modified for grazing. In fact, *Equus* is the only surviving twig of an evolutionary bush with many divergent trends.

in microevolution. Evolutionary trends can also result directly from natural selection. For example, when horse ancestors invaded the grasslands that spread during the mid-Cenozoic, there was strong selection for grazers that could escape predators by running faster. This trend would not have occurred without open grasslands.

Whatever its cause, an evolutionary trend does not imply that there is some intrinsic drive toward a particular phenotype. Evolution is the result of the interactions between organisms and their current environments; if environmental conditions change, an evolutionary trend may cease or even reverse itself. The cumulative effect of these ongoing interactions between organisms and their environments is enormous: It is through them that the staggering diversity of life—Darwin's "endless forms most beautiful"—has arisen.

CONCEPT CHECK 25.6

1. How can the Darwinian concept of descent with modification explain the evolution of such complex structures as the vertebrate eye?
2. **WHAT IF?** The myxoma virus kills up to 99.8% of infected European rabbits in populations with no previous exposure to the virus. The virus is transmitted between living rabbits by mosquitoes. Describe an evolutionary trend (in either the rabbit or virus) that might occur after a rabbit population first encounters the virus.

For suggested answers, see Appendix A.

25 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

CONCEPT 25.1

Conditions on early Earth made the origin of life possible *(pp. 526–528)*

- Experiments simulating possible early atmospheres have produced organic molecules from inorganic precursors. Amino acids, lipids, sugars, and nitrogenous bases have also been found in meteorites.
- Amino acids and RNA nucleotides polymerize when dripped onto hot sand, clay, or rock. Organic compounds can spontaneously assemble into **protocells**, membrane-bounded droplets that have some properties of cells.
- The first genetic material may have self-replicating, catalytic RNA. Early protocells containing such RNA would have increased through natural selection.

? *Describe the roles that montmorillonite clay and vesicles may have played in the origin of life.*

CONCEPT 25.2

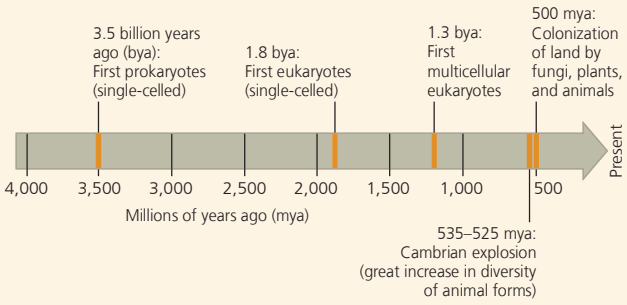
The fossil record documents the history of life *(pp. 528–532)*

- The fossil record, based largely on fossils found in sedimentary rocks, documents the rise and fall of different groups of organisms over time.
- Sedimentary strata reveal the relative ages of fossils. The ages of fossils can be estimated by **radiometric dating** and other methods.
- The fossil record shows how new groups of organisms can arise via the gradual modification of preexisting organisms.

? *What are the challenges of estimating the ages of old fossils? Explain how these challenges may be overcome in some circumstances.*

CONCEPT 25.3

Key events in life's history include the origins of unicellular and multicellular organisms and the colonization of land *(pp. 532–537)*



? *What is the "Cambrian explosion," and why is it significant?*

CONCEPT 25.4

The rise and fall of groups of organisms reflect differences in speciation and extinction rates *(pp. 537–544)*

- In **plate tectonics**, continental plates move gradually over time, altering the physical geography and climate of Earth, leading to extinctions in some groups and speciation in others.
- Evolutionary history has been punctuated by five **mass extinctions** that radically altered life's history. Possible causes for these extinctions include continental drift, volcanic activity, and impacts from asteroids.
- Large increases in the diversity of life have resulted from **adaptive radiations** that followed mass extinctions. Adaptive radiations have also occurred in groups of organisms that possessed major evolutionary innovations or that colonized new regions in which there was little competition from other organisms.

? *Explain how the broad evolutionary changes seen in the fossil record are the cumulative result of speciation and extinction events.*

CONCEPT 25.5

Major changes in body form can result from changes in the sequences and regulation of developmental genes *(pp. 544–547)*

- Developmental genes affect morphological differences between species by influencing the rate, timing, and spatial patterns of change in an organism's form as it develops into an adult.
- The evolution of new forms can be caused by changes in the nucleotide sequences or regulation of developmental genes.

? *How could changes in a single gene or DNA region ultimately lead to the origin of a new group of organisms?*

CONCEPT 25.6

Evolution is not goal oriented *(pp. 547–549)*

- Novel and complex biological structures can evolve through a series of incremental modifications, each of which benefits the organism that possesses it.
- Evolutionary trends can be caused by natural selection in a changing environment or species selection, resulting from interactions between organisms and their current environments.

? *Explain the reasoning behind the statement "Evolution is not goal oriented."*

TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

1. Fossilized stromatolites
   (A) formed around deep-sea vents.
   (B) resemble structures formed by bacterial communities that are found today in some shallow marine bays.
   (C) provide evidence that plants moved onto land in the company of fungi around 500 million years ago.
   (D) contain the first undisputed fossils of eukaryotes.

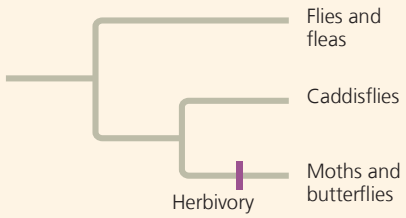
2. The oxygen revolution changed Earth's environment dramatically. Which of the following took advantage of the presence of free oxygen in the oceans and atmosphere?
   (A) the evolution of cellular respiration, which used oxygen to help harvest energy from organic molecules
   (B) the persistence of some animal groups in anaerobic habitats
   (C) the evolution of photosynthetic pigments that protected early algae from the corrosive effects of oxygen
   (D) the evolution of chloroplasts after early protists incorporated photosynthetic cyanobacteria
3. Which factor most likely caused animals and plants in India to differ greatly from species in nearby southeast Asia?
   (A) The species became separated by convergent evolution.
   (B) The climates of the two regions are similar.
   (C) India is in the process of separating from the rest of Asia.
   (D) India was a separate continent until 45 million years ago.
4. Large-scale, worldwide adaptive radiations have occurred in which of the following situations?
   (A) when there are no available ecological niches
   (B) after each of the big five mass extinctions
   (C) after colonization of an isolated island that contains suitable habitat and few competitor species
   (D) whenever an evolutionary innovation was needed for organisms to thrive
5. Scientists studying the origin of life have accomplished which of the following steps?
   (A) abiotic synthesis of protocells with self-replicating, catalytic RNA
   (B) formation of vesicles that use RNA as a template for DNA synthesis
   (C) formation of protocells that use DNA to direct the polymerization of amino acids
   (D) abiotic synthesis of RNA's bases (A, C, G, U)

Levels 3-4: Applying/Analyzing

6. A genetic change that caused a certain *Hox* gene to be expressed along the tip of a vertebrate limb bud instead of farther back helped make possible the evolution of the tetrapod limb. This type of change is illustrative of
   (A) the influence of environment on development.
   (B) paedomorphosis.
   (C) a change in a developmental gene or in its regulation that altered the spatial organization of body parts.
   (D) heterochrony.
7. A swim bladder is a gas-filled sac that helps fish maintain buoyancy. The evolution of the swim bladder from the air-breathing organ (a simple lung) of an ancestral fish is an example of
   (A) exaptation.
   (B) changes in *Hox* gene expression.
   (C) paedomorphosis.
   (D) adaptive radiation.

Levels 5-6: Evaluating/Creating

8. **EVOLUTION CONNECTION** Describe how gene flow, genetic drift, and natural selection all can influence macroevolution.
9. **SCIENTIFIC INQUIRY** Herbivory (plant eating) has evolved repeatedly in insects, typically from meat-eating or detritus-feeding ancestors (detritus is dead organic matter). Moths and butterflies, for example, eat plants, whereas their "sister group" (the insect group to which they are most closely related), the caddisflies, feed on animals, fungi, or detritus. As illustrated in the following phylogenetic tree, the combined moth/butterfly and caddisfly group shares a common ancestor with flies and fleas. Like caddisflies, flies and fleas are thought to have evolved from ancestors that did not eat plants.



   There are 140,000 species of moths and butterflies and 7,000 species of caddisflies. State a hypothesis about the impact of herbivory on adaptive radiations in insects. How could this hypothesis be tested?
10. **WRITE ABOUT A THEME: ORGANIZATION** You have seen many examples of how form fits function at all levels of the biological hierarchy. However, we can imagine forms that would function better than some forms actually found in nature. For example, if the wings of a bird were not formed from its forelimbs, such a hypothetical bird could fly yet also hold objects with its forelimbs. In a short essay (100–150 words), use the concept of "evolution as tinkering" to explain why there are limits to the functionality of forms in nature.
11. **SYNTHESIZE YOUR KNOWLEDGE**



   In 2010, the Soufriere Hills volcano on the Caribbean island of Montserrat erupted violently, spewing huge clouds of ash and gases into the sky. Explain how the volcanic eruptions at the end of the Permian period and the formation of Pangaea, both of which occurred about 252 million years ago, set in motion events that altered evolutionary history.

For selected answers, see Appendix A.

Explore Scientific Papers with Science in the Classroom AAAS
How has adaptive evolution occurred in stickleback fish?
Go to "What the Pelvis Can Teach Us about Evolution"
at www.scienceintheclassroom.org.
Instructors: Questions can be assigned in Mastering Biology.

Unit 5 THE EVOLUTIONARY HISTORY OF BIOLOGICAL DIVERSITY



Sallie (Penny) Chisholm, Institute Professor in Civil and Environmental Engineering at the Massachusetts Institute of Technology, has received the 2011 National Medal of Science, the 2019 Crafoord Prize in Biosciences, and many other prestigious awards. Dr. Chisholm received a B.A. in Biology and Chemistry from Skidmore College and a Ph.D. in Biology from the State University of New York, Albany. Elected to the U.S. National Academy of Sciences in 2003, Dr. Chisholm has a long-standing interest in the essential roles that photosynthetic microbes play in marine ecosystems. Currently, she and her students are studying these organisms from the genome to global scale.

AN INTERVIEW WITH

Penny Chisholm

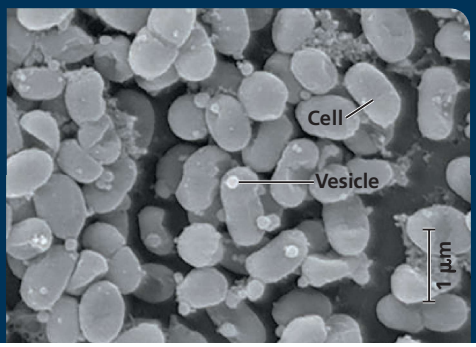
How did you first become interested in science?

I grew up in Michigan's Upper Peninsula, in the sticks. Growing up, my family was all about business; I wasn't from an academic background. So, when I started studying biology in college, I was kind of surprised to find out that I liked science as a way of knowing. I had never been exposed to doing experiments and discovering new things on your own. I had the chance to do an independent research project on a local lake to measure its manganese budget. We measured the movement of manganese into and out of the lake over the course of a year, drilling holes in the ice to sample in winter. All of this was really cool and got me excited about the dynamics of aquatic ecosystems. Once I looked under the microscope and saw a world that I didn't even know existed—the microbes living in lakes—there was no turning back.

Much of your research is on the bacterium *Prochlorococcus*. Tell us about this organism.

Prochlorococcus is the smallest photosynthetic cell on the planet and the most abundant—it is less than 1/100th the width of a human hair, and there are over a billion billion billion of these tiny cells in the ocean! *Prochlorococcus* feeds small protists, which in turn are eaten by larger marine organisms, and thus they play a key role in ocean ecosystems. And when *Prochlorococcus* cells are infected by viruses, they break apart and their organic compounds serve as a food source for other bacteria in the ocean. Despite these organisms' importance, we didn't even know they existed when I was a student. And then, in the mid-1980s, I was fortunate enough to be involved in their discovery. I was fascinated by them—they were almost everywhere in the oceans. Eventually we learned to grow them in the lab. I was hooked!

▼ *Prochlorococcus* cells and vesicles.



What has *Prochlorococcus* taught you?

We've known for a long time about diatoms and other relatively large photosynthetic organisms—phytoplankton—in the ocean. Those organisms were like the trees and the bushes. Suddenly, with the discovery of small photosynthetic bacteria such as *Prochlorococcus*, we learned, "Oh! There's grass, too!" Once we knew *Prochlorococcus* was there, we developed methods to monitor it in the field and sort out individual cells. We wondered how a single species could be so abundant in so many different areas of the ocean. We found out that this organism has extremely high levels of genetic diversity. This enables it to thrive in many different ocean environments, despite ever-changing conditions. Overall, studying *Prochlorococcus* has taught me to be humbled by the mind-blowing complexity of the natural world.

> ***"Studying* Prochlorococcus *has taught me to be humbled by the mind-blowing complexity of the natural world."***

To date, what is the most surprising discovery from your lab?

The discovery of "grass" in the ocean was certainly a surprise! More recently, we've learned that the ocean is full of vesicles, very small lipid-bound particles that are budded off a cell. They look like little round peas on top of the cell. For years I had a picture of them that one of my students had taken, and I would ask people, "What do you think this is?" No one knew, until one of my post-docs speculated that they were vesicles, and demonstrated this to be true. He discovered that they contain DNA, as well as RNA and a variety of proteins and lipids. We can determine which species produced a vesicle by sequencing the DNA it contains. We found out that many different species are producing vesicles. This is a beautiful example of how a casual observation in the lab—a photograph that I kept in a file cabinet for years—eventually led to the discovery of a new component of ocean ecosystems. Now the challenge is figuring out what they are doing!

What do you find most rewarding about your job?

Working with *Prochlorococcus* is such a gift! Over the years, it's been an almost endless process of discovery—the organism is such a fundamental part of life in the ocean, and there are so many different questions you can ask. It has also been fruitful and exciting to work on *Prochlorococcus* with students and colleagues from many different backgrounds. It is wonderful to see my students working together to answer really hard questions. And I've learned so much from them—it has been a privilege and a joy to help them discover what they're best at and what they really enjoy doing. I love what I do. What could be more important than studying life?

26 Phylogeny and the Tree of Life

KEY CONCEPTS

26.1 **Phylogenies show evolutionary relationships** *p. 554*

26.2 **Phylogenies are inferred from morphological and molecular data** *p. 558*

26.3 **Shared characters are used to construct phylogenetic trees** *p. 559*

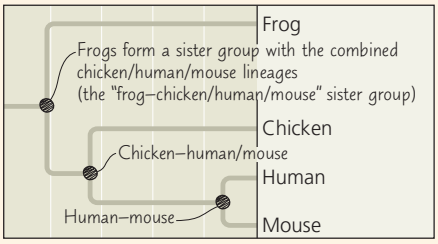
26.4 **An organism's evolutionary history is documented in its genome** *p. 565*

26.5 **Molecular clocks help track evolutionary time** *p. 566*

26.6 **Our understanding of the tree of life continues to change based on new data** *p. 568*

Study Tip

Label a drawing: The members of a *sister group* are each other's closest relatives, making sister groups a useful way to describe evolutionary relationships. As in this example, identify the sister groups associated with each branch point in Figures 26.11, 26.12, 26.14, and 26.16.



Go to Mastering Biology

For Students (in eText and Study Area)
- Get Ready for Chapter 26
- Figure 26.12 Walkthrough: Using Derived Characters to Infer Phylogeny

For Instructors to Assign (in Item Library)
- Misconception Questions 126, 128, 129
- Tutorial: Visualizing Phylogenetic Relationships

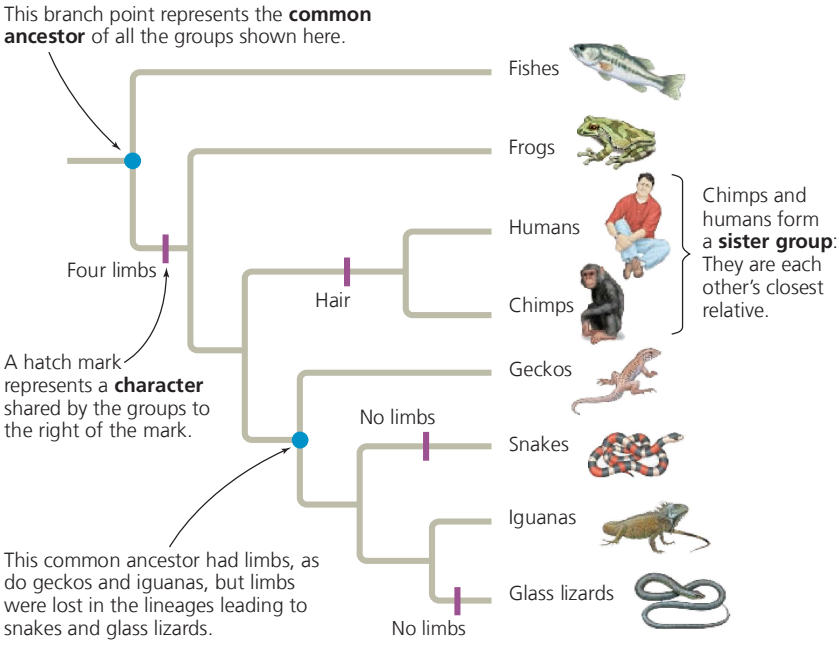
Ready-to-Go Teaching Module (in Instructor Resources)
- Phylogenetic Trees (Concept 26.3)



Figure 26.1 Although this animal resembles a snake, it is actually a legless lizard: the glass lizard *Ophisaurus apodus*. Why isn't the glass lizard considered a snake? Biologists based this decision in part on a comparison of its traits with those of snakes—and the glass lizard does not have a highly mobile jaw or many vertebrae, two traits shared by all snakes.

How do biologists distinguish and categorize the millions of species on Earth?

Traits shared due to **common ancestry** are used to classify organisms into groups that reflect their **evolutionary history**:



CONCEPT 26.1

Phylogenies show evolutionary relationships

The glass lizard in Figure 26.1 is part of the continuum of life extending from the earliest organisms to the great variety of species alive today. In this unit, we will survey this diversity and describe hypotheses regarding how it evolved.

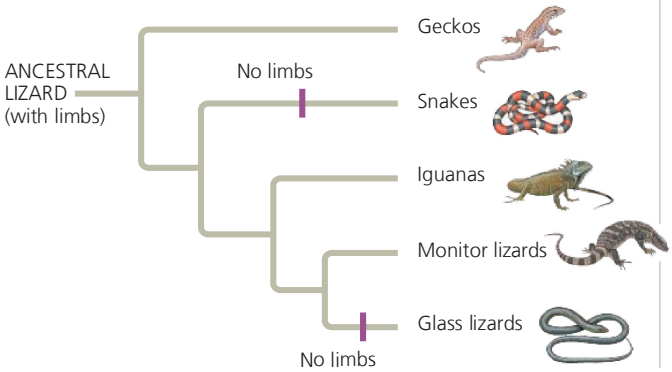
To set the stage for surveying life's diversity, in this chapter we consider how biologists trace **phylogeny**, the evolutionary history of a species or group of species. A phylogeny of lizards and snakes, for example, indicates that both glass lizards and snakes evolved from lizards with legs—but they evolved from different lineages of legged lizards **(Figure 26.2)**. Thus, it appears that their legless conditions evolved independently. As we'll see, biologists reconstruct phylogenies like that in Figure 26.2 using **systematics**, a discipline focused on classifying organisms and determining their evolutionary relationships. We'll begin by describing how organisms are named.

Binomial Nomenclature

Common names for organisms—such as monkey, finch, and lilac—convey meaning in casual usage, but they can also cause confusion. Each of these names, for example, refers to more than one species. Moreover, some common names do not accurately reflect the kind of organism they signify. Consider these three "fishes": jellyfish (a cnidarian), crayfish (a small, lobster-like crustacean), and silverfish (an insect). And, of course, a given organism has different names in different languages.

To avoid ambiguity when communicating about their research, biologists refer to organisms by Latin scientific names. The two-part format of the scientific name, commonly called a **binomial**, was instituted in the 18th century by Carolus Linnaeus (see Concept 22.1). The first part of a binomial is the name of the **genus** (plural, *genera*) to which the species belongs. The second part, called the specific epithet, is unique for each species within the genus. An example of a binomial is *Panthera pardus*, the scientific name for the leopard. Notice that the first letter of the genus is capitalized and the entire binomial is italicized. (Newly created scientific names are also "latinized": You can name an insect you discover after a friend, but you must add a Latin ending.) Many of the more than 11,000 binomials assigned by Linnaeus are still used today, including the optimistic name he gave our own species—*Homo sapiens*, meaning "wise man."

▼ **Figure 26.2 Convergent evolution of limbless bodies.** A phylogeny based on DNA sequence data reveals that a legless body form evolved independently from legged ancestors in the lineages leading to glass lizards and to snakes.



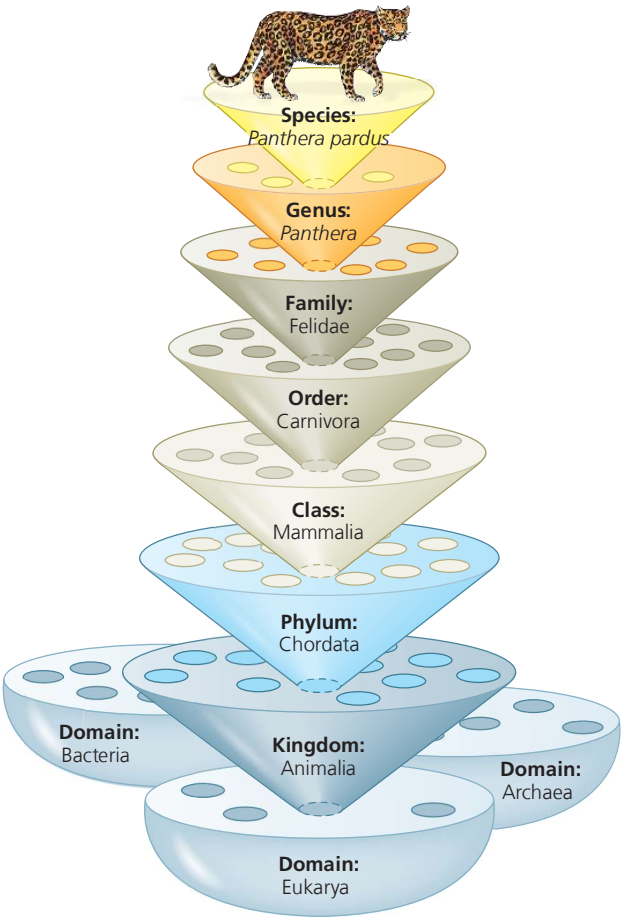
Hierarchical Classification

In addition to naming species, Linnaeus also grouped them into a hierarchy of increasingly inclusive categories. The first grouping is built into the binomial: Species that appear to be closely related are grouped into the same genus. For example, the leopard (*Panthera pardus*) belongs to a genus that also includes the African lion (*Panthera leo*), the tiger (*Panthera tigris*), and the jaguar (*Panthera onca*). Beyond genera, biologists employ progressively more comprehensive categories of classification. The classification system named after Linnaeus, the Linnaean system, places related genera in the same **family**, families into **orders**, orders into **classes**, classes into **phyla** (singular, *phylum*), phyla into **kingdoms**, and, more recently, kingdoms into **domains (Figure 26.3)**. The resulting biological classification of a particular organism is somewhat like a postal address identifying a person in a particular apartment, in a building with many apartments, on a street with many apartment buildings, in a city with many streets, and so on.

The named group at any level of the hierarchy is called a **taxon** (plural, *taxa*). In the leopard example, *Panthera* is a taxon at the genus level, and Mammalia is a taxon at the class level that includes all the many orders of mammals. Note that in the Linnaean system, taxa broader than the genus are not italicized, though they are capitalized.

Classifying species is a way to structure our human view of the world. We lump together various species of trees to which we give the common name of pines and distinguish them from other trees that we call firs. Systematists have decided that pines and firs are different enough to be placed in separate genera, yet similar enough to be grouped into the same family, Pinaceae. As with pines and firs, higher levels of classification are usually defined by particular characters chosen by systematists. However, characters that are useful for classifying one group of organisms may not be appropriate for other organisms. For this reason, the larger categories often are not comparable between lineages; that is, an order of snails does not exhibit the same degree of morphological or genetic diversity as an order of mammals. As we'll see, the placement of species into orders, classes, and so on also does not necessarily reflect evolutionary history.

▼ **Figure 26.3 Linnaean classification.** At each level, or "rank," species are placed in groups within more inclusive groups.

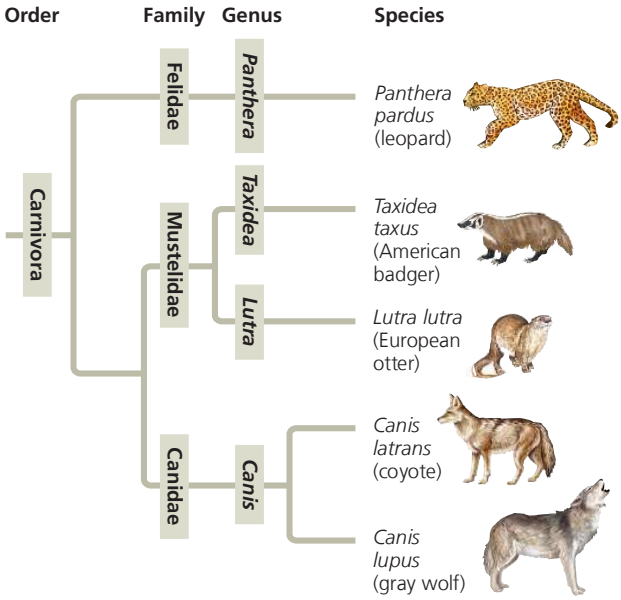


Linking Classification and Phylogeny

The evolutionary history of a group of organisms can be represented in a branching diagram called a **phylogenetic tree**. As in **Figure 26.4**, the branching pattern often matches how systematists have classified groups of organisms nested within more inclusive groups. Sometimes, however, systematists have placed a species within a genus (or other group) to which it is *not* most closely related. One reason for such a mistake might be that over the course of evolution, a species has lost a key feature shared by its close relatives. If DNA or other new evidence indicates that an organism has been misclassified, the organism may be reclassified to accurately reflect its evolutionary history. Another issue is that while the Linnaean system may distinguish groups, such as amphibians, mammals, reptiles, and other classes of vertebrates, it tells us nothing about these groups' evolutionary relationships to one another.

Such difficulties in aligning Linnaean classification with phylogeny have led many systematists to propose that classification be based entirely on evolutionary relationships. In such systems, names are assigned only to groups that include a common ancestor and all of its descendants. Using this approach, some commonly recognized groups become part of other groups previously at the same level of the Linnaean system. For example, because birds evolved from a group of reptiles, Aves (the Linnaean class to which birds are assigned) is considered a subgroup of Reptilia (also a class in the Linnaean system).

▼ **Figure 26.4 The connection between classification and phylogeny.** Hierarchical classification can reflect the branching patterns of phylogenetic trees. This tree shows evolutionary relationships between some of the taxa within order Carnivora, itself a branch of class Mammalia.



What We Can and Cannot Learn from Phylogenetic Trees

Regardless of how groups are named, a phylogenetic tree represents a hypothesis about evolutionary relationships. These relationships often are depicted as a series of dichotomies, or two-way branch points. Each **branch point** represents the common ancestor of the two evolutionary lineages diverging from it. An **evolutionary lineage** is a sequence of ancestral organisms leading to a particular descendant taxon. **Figure 26.5** illustrates these elements of a phylogenetic tree and offers more tips on interpreting these diagrams.

Each tree in Figure 26.5 has a branch point that represents the common ancestor of chimpanzees and humans. Chimps and humans are an example of **sister taxa**, groups of organisms that share an immediate common ancestor that is not shared by any other group. Note that there is a sister group associated with each branch point in a tree (since each branch point represents the common ancestor of the lineages diverging from it).

The members of a sister group are each other's closest relatives, making sister groups a useful way to describe the

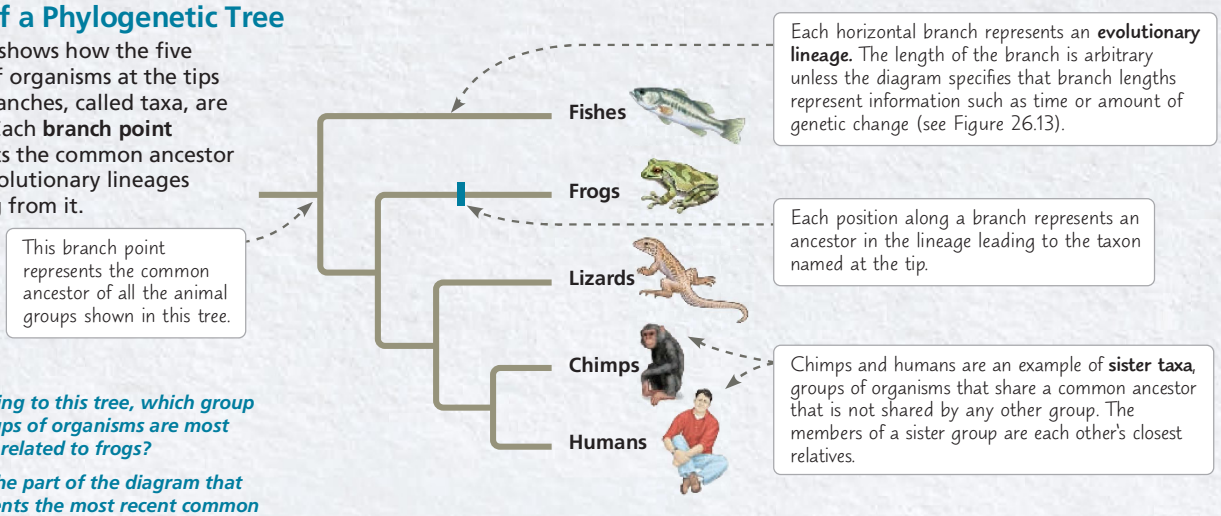
▼ Figure 26.5 VISUALIZING PHYLOGENETIC RELATIONSHIPS

A phylogenetic tree visually represents a hypothesis of how a group of organisms are related. This figure explores how the way a tree is drawn conveys information.

Instructors: Additional questions related to this Visualizing Figure can be assigned in **Mastering Biology**.

Parts of a Phylogenetic Tree

This tree shows how the five groups of organisms at the tips of the branches, called taxa, are related. Each **branch point** represents the common ancestor of the evolutionary lineages diverging from it.

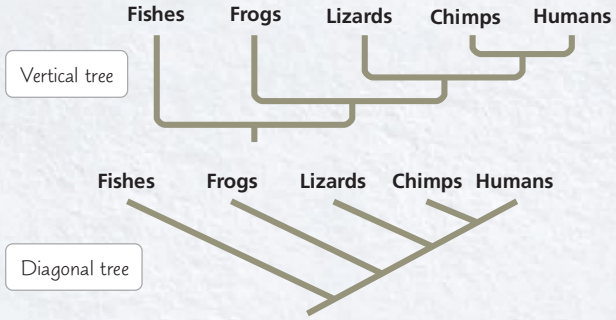


1. ***According to this tree, which group or groups of organisms are most closely related to frogs?***

2. ***Label the part of the diagram that represents the most recent common ancestor of frogs and humans.***

Alternative Forms of Tree Diagrams

These diagrams are referred to as "trees" because they use the visual analogy of branches to represent evolutionary lineages diverging over time. In this text, trees are usually drawn horizontally, as shown above, but the same tree can be drawn vertically or diagonally without changing the relationships it conveys.

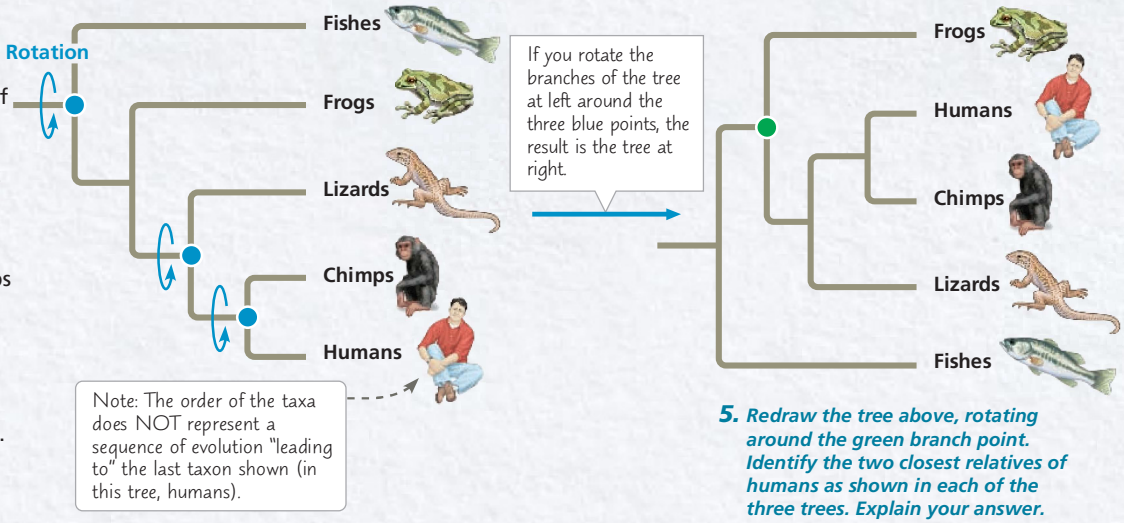


3. ***How many sister taxa are shown in these two trees? Identify them.***

4. ***Redraw the horizontal tree in Figure 26.2 as a vertical tree and a diagonal tree.***

Rotating Around Branch Points

Rotating the branches of a tree around a branch point does not change what they convey about evolutionary relationships. As a result, the order in which taxa appear at the branch tips is not significant. What matters is the branching pattern, which signifies the order in which the lineages have diverged from common ancestors.



5. ***Redraw the tree above, rotating around the green branch point. Identify the two closest relatives of humans as shown in each of the three trees. Explain your answer.***

evolutionary relationships shown in a tree. For example, in Figure 26.5, the evolutionary lineage leading to lizards shares an immediate common ancestor with the lineage leading to chimpanzees and humans. Thus, we can describe this portion of the tree by saying that lizards are the sister taxon to a group consisting of chimpanzees and humans.

As also discussed in Figure 26.5, the branches of a tree can be rotated around branch points without changing the relationships shown in the tree. That is, the order in which the taxa appear at the right side of the tree does not represent a *sequence* of evolution—in this case, it does not imply a sequence leading from fishes to humans.

This tree, like all of the phylogenetic trees in this book, is **rooted**, which means that a branch point within the tree (often drawn farthest to the left) represents the most recent common ancestor of all taxa in the tree. A lineage that diverges from all other members of its group early in the history of the group is called a **basal taxon**. Hence, like the fishes in Figure 26.5, a basal taxon lies on one of the two branches diverging from the branch point that represents the common ancestor of the group. In general, the lineages represented by these two branches originated at the same point in time and hence have been evolving for the same length of time.

What other key points do we need to keep in mind when interpreting phylogenetic trees? First, they are intended to show patterns of descent, not phenotypic similarity. Although closely related organisms often resemble one another due to their common ancestry, they may not if their lineages have evolved at different rates or faced very different environmental conditions. For example, even though crocodiles are more closely related to birds than to lizards (see Figure 22.17), they look more like lizards because morphology has changed dramatically in the bird lineage.

Second, we cannot necessarily infer the ages of the taxa or branch points shown in a tree. For example, the tree in Figure 26.5 does not indicate that chimpanzees evolved before humans. Rather, the tree shows only that chimpanzees and humans share a recent common ancestor, but we cannot tell when that ancestor lived or when the first chimpanzees or humans arose. Generally, unless we are given specific information about what the branch lengths in a tree mean—for example, that they are proportional to time—we should interpret the diagram solely in terms of patterns of descent. No assumptions should be made about when particular species evolved or how much change occurred in each lineage.

Third, we should not assume that a taxon on a phylogenetic tree evolved from the taxon next to it. Figure 26.5 does not indicate that humans evolved from chimpanzees or vice versa. We can infer only that the lineage leading to humans and the lineage leading to chimpanzees both evolved from a recent common ancestor. That ancestor, which is now extinct, was neither a human nor a chimpanzee.

Applying Phylogenies

Understanding phylogeny can have practical applications. Consider maize (corn), which originated in the Americas and is now an important food crop worldwide. From a phylogeny of maize based on DNA data, researchers have identified two species of wild grasses that may be maize's closest living relatives. These two close relatives may be useful as "reservoirs" of beneficial alleles that can be transferred to cultivated maize by cross-breeding or genetic engineering.

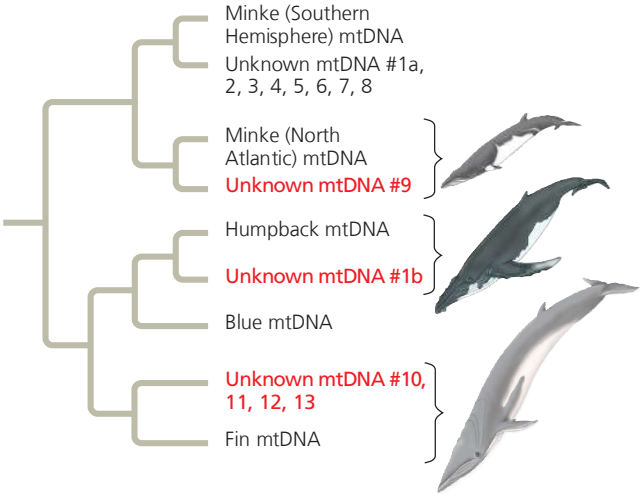
A different use of phylogenetic trees is to infer species identities by analyzing the relatedness of DNA sequences from different organisms. Researchers have used this approach to investigate whether "whale meat" had been harvested illegally from whale species protected under international law rather than from species that can be harvested legally **(Figure 26.6)**.

▼ Figure 26.6 Inquiry

What is the species identity of food being sold as whale meat?

Experiment C. S. Baker and S. R. Palumbi purchased 13 samples of "whale meat" from Japanese fish markets. They sequenced part of the mitochondrial DNA (mtDNA) from each sample and compared their results with the comparable mtDNA sequence from known whale species. To infer the species identity of each sample, the team constructed a *gene tree*, a phylogenetic tree that shows patterns of relatedness among DNA sequences rather than among taxa.

Results Of the species in the resulting gene tree, only Minke whales caught in the Southern Hemisphere can be sold legally in Japan.



Conclusion This analysis indicated that mtDNA sequences of six of the unknown samples (in red) were most closely related to mtDNA sequences of whales that are not legal to harvest.

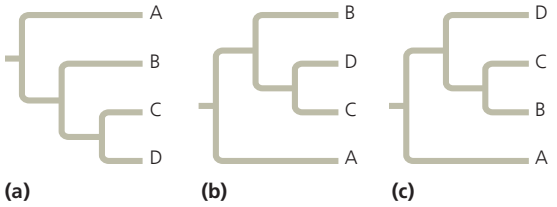
Data from C. S. Baker and S. R. Palumbi, Which whales are hunted? A molecular genetic approach to monitoring whaling, *Science* 265:1538–1539 (1994). Reprinted with permission from AAAS.

WHAT IF? *What different results would have indicated that all of the whale meat had been harvested legally?*

How do researchers construct phylogenetic trees like those we've considered here? In the next section, we'll begin to answer that question by examining the data used to determine phylogenies.

CONCEPT CHECK 26.1

1. **VISUAL SKILLS** Based on the tree in Figure 26.4, are leopards more closely related to badgers or wolves, or are they equally related to these two species? Explain.
2. **VISUAL SKILLS** Which of the trees shown here depicts an evolutionary history different from the other two? Explain.



3. **DRAW IT** The bear family (Ursidae) is more closely related to the badger/otter family (Mustelidae) than to the dog family (Canidae). Use this information to redraw Figure 26.4.

For suggested answers, see Appendix A.

CONCEPT 26.2

Phylogenies are inferred from morphological and molecular data

To infer phylogeny, systematists must gather as much information as possible about the morphology, genes, and biochemistry of the relevant organisms. It is important to focus on features that result from common ancestry because only those features reflect evolutionary relationships.

Morphological and Molecular Homologies

Recall that phenotypic and genetic similarities due to shared ancestry are called **homologies**. For example, the similarity in the number and arrangement of bones in the forelimbs of mammals is due to their descent from a common ancestor with the same bone structure; this is an example of a morphological homology (see Figure 22.15). In the same way, genes or other DNA sequences are homologous if they are descended from sequences carried by a common ancestor.

In general, organisms that share very similar morphologies or similar DNA sequences are likely to be more closely related than organisms with vastly different structures or sequences. In some cases, however, the morphological divergence between related species can be great and their genetic divergence small (or vice versa). Consider the Hawaiian silversword plants: some of these species are tall, twiggy trees, while others are dense, ground-hugging shrubs (see Figure 25.23). But despite these striking phenotypic differences, the silverswords' genes are very similar. Based on these small molecular divergences, scientists estimate that the silversword group began to diverge 5 million years ago. We'll discuss how scientists use molecular data to estimate such divergence times later in this chapter.

Sorting Homology from Analogy

A potential source of confusion in constructing a phylogeny is similarity between organisms that is due to convergent evolution—called **analogy**—rather than to shared ancestry (homology). Convergent evolution occurs when similar environmental pressures and natural selection produce similar (analogous) adaptations in organisms from different evolutionary lineages. For example, the two mole-like animals shown in **Figure 26.7** look very similar. However, their internal anatomy, physiology, and reproductive systems are very dissimilar. Indeed, genetic and fossil evidence indicate that the common ancestor of these animals lived 160 million years ago. This common ancestor and most of its descendants were not mole-like. It appears that analogous characteristics evolved independently in these two lineages as they became adapted to similar lifestyles—hence, the similar features of these animals should not be considered when reconstructing their phylogeny.

Another clue to distinguishing between homology and analogy is the complexity of the characters being compared. The more elements that are similar in two complex structures, the more likely it is that the structures evolved from a common ancestor. For instance, the skulls of an adult human and an adult chimpanzee both consist of many bones fused together. The compositions of the skulls match almost perfectly, bone for bone. It is highly improbable that such complex structures, matching in so many details, have separate origins. More likely, the genes involved in the development of both skulls were inherited from a common ancestor.

The same argument applies to comparisons at the gene level. Genes are sequences of thousands of nucleotides, each of which represents an inherited character in the form of one of the four DNA bases: A (adenine), G (guanine), C (cytosine), or T (thymine). If genes in two organisms share many portions of their nucleotide sequences, it is likely that the genes are homologous.



▶ Figure 26.7 Convergent evolution in burrowers. A long body, large front paws, small eyes, and a pad of thick skin that protects the nose all evolved independently in these species.

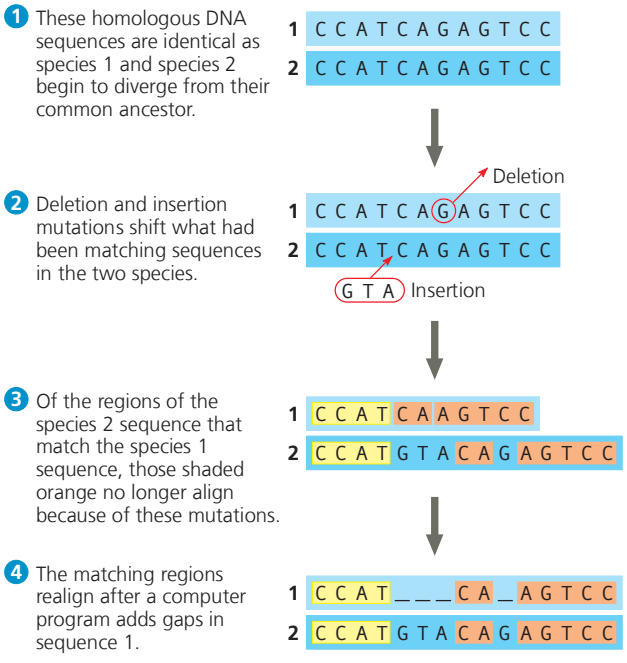
Evaluating Molecular Homologies

Comparing DNA molecules often poses technical challenges for researchers. The first step after sequencing the DNA is to align comparable sequences from the species being studied. If the species are very closely related, the sequences probably differ at only one or a few sites. In contrast, comparable nucleic acid sequences in distantly related species usually have different bases at many sites and may have different lengths. This is because insertions and deletions accumulate over long periods of time.

Suppose, for example, that certain noncoding DNA sequences near a particular gene are very similar in two species, except that the first base of the sequence has been deleted in one of the species. The effect is that the remaining sequence shifts back one notch. A comparison of the two sequences that does not take this deletion into account would overlook what in fact is a very good match. Computer programs can be used to identify such matches by testing possible alignments for comparable DNA segments of differing lengths **(Figure 26.8)**.

Such molecular comparisons reveal that many base substitutions and other differences have accumulated in the comparable genes of an Australian "mole" and a golden mole. The many differences indicate that their lineages have diverged greatly since their common ancestor; thus, we say that the living species are not closely related. In contrast, the high degree of gene sequence similarity among the silversword plants indicates that they are all very closely related, in spite of their considerable morphological differences.

▼ Figure 26.8 Aligning segments of DNA. Systematists search for similar sequences along DNA segments from two species (only one DNA strand is shown for each species). In this example, 11 of the original 12 bases have not changed since the species diverged. Hence, those portions of the sequences still align once the length is adjusted.



▼ Figure 26.9 A coincidental match. These two DNA sequences from distantly related species coincidentally share 23% of their bases (those highlighted in yellow).

A C G G A T A G T C C A C T A G G C A C T A
T C A C C G A C A G G T C T T T G A C T A G

WHAT IF? *Why might you expect organisms that are not closely related to nevertheless share roughly 25% of their bases?*

Just as with morphological characters, it is necessary to distinguish homology from analogy in evaluating molecular similarities for evolutionary studies. Two sequences that resemble each other at many points along their length most likely are homologous (see Figure 26.8). But in organisms that do not appear to be closely related, the bases that their otherwise very different sequences happen to share may simply be coincidental matches **(Figure 26.9)**. Scientists have developed statistical tools that can help distinguish "distant" homologies from such coincidental matches in extremely divergent sequences.

CONCEPT CHECK 26.2

1. Decide whether each of the following pairs of structures more likely represents analogy or homology, and explain your reasoning: (a) a porcupine's quills and a cactus's spines; (b) a cat's paw and a human's hand; (c) an owl's wing and a hornet's wing.
2. **WHAT IF?** Suppose that two species, A and B, have similar appearances but very divergent gene sequences, while species B and C have very different appearances but similar gene sequences. Which pair of species is more likely to be closely related: A and B or B and C? Explain.

For suggested answers, see Appendix A.

CONCEPT 26.3

Shared characters are used to construct phylogenetic trees

As we've discussed, a key step in reconstructing phylogenies is to distinguish homologous features from analogous ones (since only homology reflects evolutionary history). Next, we'll describe cladistics, a widely used set of methods for inferring phylogeny.

Cladistics

In the approach to systematics called **cladistics**, common ancestry is the primary criterion used to classify organisms. Using this methodology, biologists attempt to place species into groups called **clades**, each of which includes an ancestral species and all of its descendants. Clades, like the categories of the Linnaean system, are nested within larger clades. In

▼ Figure 26.10 Monophyletic, paraphyletic, and polyphyletic groups.

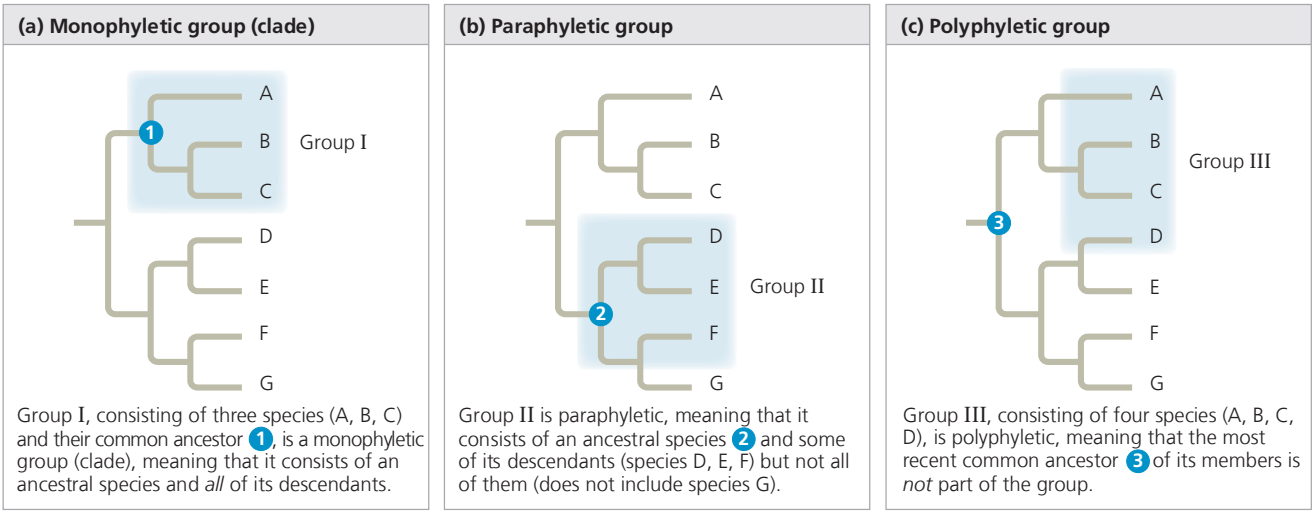


Figure 26.4, for example, the cat group (Felidae) represents a clade within a larger clade (Carnivora) that also includes the dog group (Canidae).

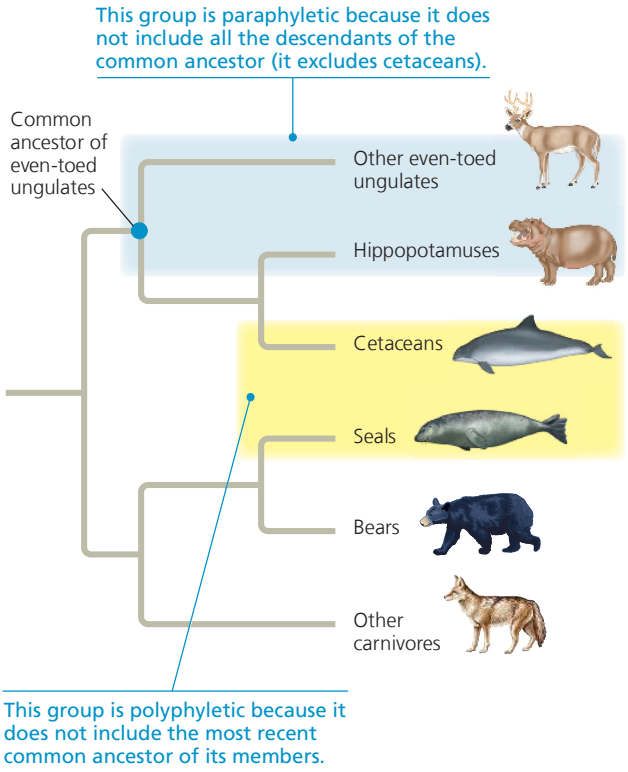
A taxon is equivalent to a clade only if it is **monophyletic** (from the Greek, meaning "single tribe"), signifying that it consists of an ancestral species and all of its descendants **(Figure 26.10a)**. Contrast this with a **paraphyletic** ("beside the tribe") group, which consists of an ancestral species and some, but not all, of its descendants **(Figure 26.10b)**, or a **polyphyletic** ("many tribes") group, which includes distantly related species but does not include their most recent common ancestor **(Figure 26.10c)**.

Note that in a paraphyletic group, the most recent common ancestor of all members of the group *is* part of the group, whereas in a polyphyletic group the most recent common ancestor *is not* part of the group. For example, a group consisting of even-toed ungulates (hippopotamuses, deer, and their relatives) and their common ancestor is paraphyletic because it does not include cetaceans (whales, dolphins, and porpoises), which descended from that ancestor **(Figure 26.11)**. In contrast, a group consisting of seals and cetaceans (based on their similar body forms) is polyphyletic because it does not include the common ancestor of seals and cetaceans. Biologists avoid defining such polyphyletic groups; if new evidence indicates that an existing group is polyphyletic, its members are reclassified.

Shared Ancestral and Shared Derived Characters

As a result of descent with modification, organisms have characters they share with their ancestors, and they also have characters that differ from those of their ancestors. For example, all mammals have backbones, but a backbone does not distinguish mammals from other vertebrates because *all* vertebrates have backbones. The backbone predates the branching of mammals from other vertebrates. Thus for mammals, the backbone is a **shared ancestral character**, a character that originated in an ancestor of the taxon. In contrast, hair is a character shared by all mammals but *not* found in their ancestors. Thus, in mammals, hair is considered a **shared derived character**, an evolutionary novelty unique to a clade.

▼ Figure 26.11 Paraphyletic versus polyphyletic groups.



DRAW IT *Circle the branch point that represents the most recent common ancestor of cetaceans and seals. Explain why that ancestor would not be part of a cetacean–seal group defined by similar body form.*

Note that a shared derived character can refer to the loss of a feature, such as the loss of limbs in snakes or whales. Also, keep in mind that it is a relative matter whether a character is considered ancestral or derived. A backbone can also qualify as a shared derived character, but only at a deeper branch point that distinguishes all vertebrates from other animals.

Inferring Phylogenies Using Derived Characters

Shared derived characters are unique to particular clades. Because all features of organisms arose at some point in the history of life, it should be possible to determine the clade in which each shared derived character first appeared and to use that information to infer evolutionary relationships.

To give an example of this approach, consider the set of characters shown in **Figure 26.12a** for each of five vertebrates—a leopard, turtle, frog, bass, and lamprey (a jawless aquatic vertebrate). As a basis of comparison, we need to select an outgroup. An **outgroup** is a species or group of species from an evolutionary lineage that is closely related to but not part of the group of species that we are studying (the **ingroup**). A suitable outgroup can be determined based on evidence from morphology, paleontology, embryonic development, and gene sequences. An appropriate outgroup for our example is the lancelet, a small animal that lives in mudflats and (like vertebrates) is a member of the more inclusive group called the chordates. Unlike the vertebrates, however, the lancelet does not have a backbone.

In our analysis, a character found in both the outgroup and the ingroup is assumed to be ancestral. We'll also assume that each derived character in Figure 26.12a arose only once in the ingroup. Thus, for a character that only occurs in a subset of the ingroup, we'll assume that the character arose in the lineage leading to those members of the ingroup.

By comparing members of the ingroup with each other and with the outgroup, we can determine which characters were derived at the various branch points of vertebrate evolution. In our example, *all* of the vertebrates in the ingroup have backbones: This character was present in the ancestral vertebrate, but not in the outgroup. Now note that hinged jaws are absent in the outgroup and in lampreys, but present in all other members of the ingroup. This indicates that hinged jaws arose in a lineage leading to all members of the ingroup *except* lampreys. Hence, we can conclude that lampreys are the sister taxon to the other vertebrates in the ingroup. Proceeding in this way, we can translate the data in our table of characters into a phylogenetic tree that places all the ingroup taxa into a hierarchy based on their derived characters **(Figure 26.12b)**.

Phylogenetic Trees with Proportional Branch Lengths

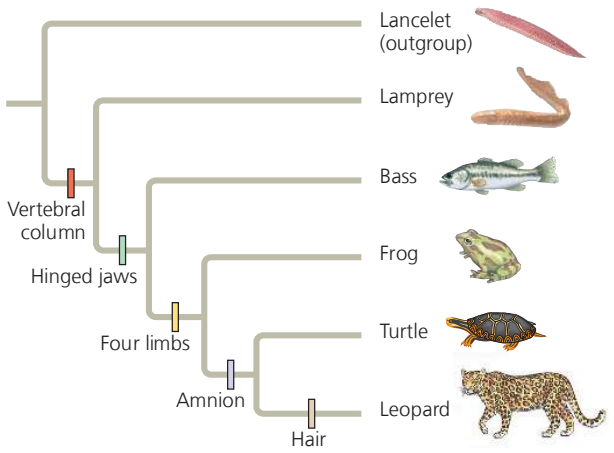
In the phylogenetic trees we have presented so far, the lengths of the tree's branches do not indicate the degree of evolutionary change in each lineage. Furthermore, the chronology represented by the branching pattern of the tree is relative (earlier versus later) rather than absolute (how many millions of years ago). But in some tree diagrams, branch lengths are proportional to the amount of evolutionary change or to the times at which particular events occurred.

▼ Figure 26.12 Using derived characters to infer phylogeny. The derived characters used here include the amnion, a membrane that encloses the embryo inside a fluid-filled sac (see Figure 34.26). Note that a different set of characters could lead us to infer a different phylogenetic tree.

TAXA

CHARACTERS	Lancelet (outgroup)	Lamprey	Bass	Frog	Turtle	Leopard
Vertebral column (backbone)	0	1	1	1	1	1
Hinged jaws	0	0	1	1	1	1
Four limbs	0	0	0	1	1	1
Amnion	0	0	0	0	1	1
Hair	0	0	0	0	0	1

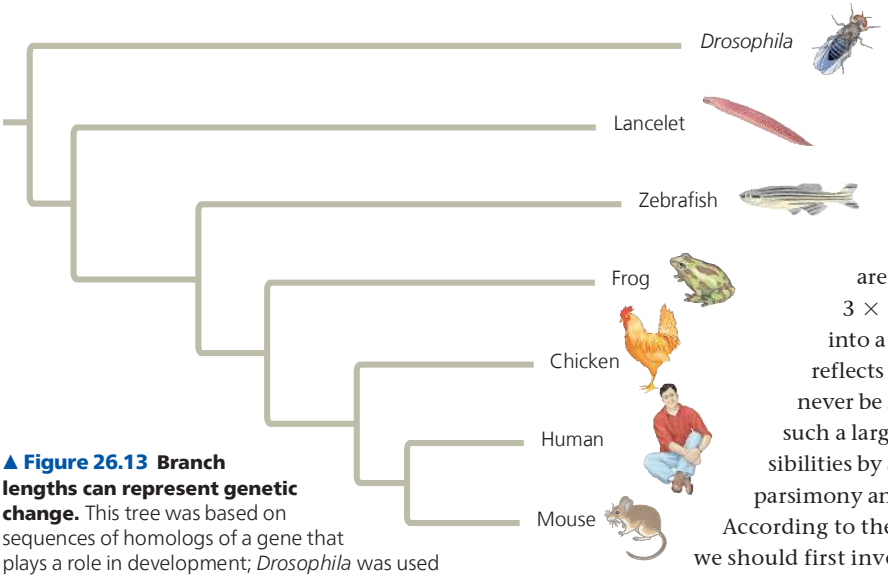
(a) Character table. A 0 indicates that a character is absent; a 1 indicates that a character is present.



(b) Phylogenetic tree. The character table in (a) leads us to infer the phylogenetic relationships shown in this tree.

DRAW IT *In (b), circle the most inclusive clade for which a hinged jaw is a shared ancestral character.*

Mastering Biology Figure Walkthrough



▲ **Figure 26.13 Branch lengths can represent genetic change.** This tree was based on sequences of homologs of a gene that plays a role in development; *Drosophila* was used as an outgroup. Branch lengths are proportional to the amount of genetic change in each lineage; varying branch lengths indicate that the gene has evolved at different rates in different lineages.

INTERPRET THE DATA *In which vertebrate lineage has the studied gene evolved most rapidly? Explain.*

In **Figure 26.13**, for example, each branch length of the phylogenetic tree reflects the number of changes that have taken place in a particular DNA sequence in that lineage. Note that the total length of the horizontal lines from the base of the tree to the mouse is less than that of the line leading to the fruit fly, *Drosophila*. This indicates that fewer genetic changes have occurred in the mouse lineage than in the *Drosophila* lineage. In addition, because the mouse and fly lineages have evolved for an equal amount of time after they diverged from a common ancestor, the *rate* of change was lower in mouse lineage than in the *Drosophila* lineage.

In general, although the branches of a phylogenetic tree may have different lengths, among organisms alive today, all the different lineages that descend from a common ancestor have survived for the same number of years. To take an extreme example, humans and bacteria had a common ancestor that lived over 3 billion years ago. Fossils and genetic evidence indicate that this ancestor was a single-celled prokaryote. Even though bacteria have apparently changed little in their morphology since that common ancestor, there have nonetheless been 3 billion years of evolution in the bacterial lineage, just as there have been 3 billion years of evolution in the lineage that ultimately gave rise to humans.

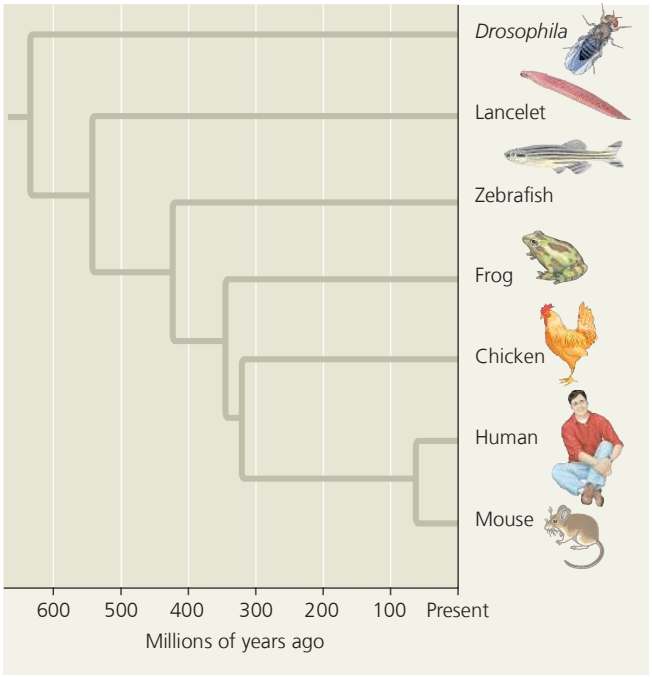
These equal spans of chronological time can be represented in a phylogenetic tree whose branch lengths are proportional to time **(Figure 26.14)**. Such a tree draws on fossil data to place branch points in the context of geologic time. Additionally, it is possible to combine these two types of trees by labeling branch points with information about rates of genetic change or dates of divergence.

Maximum Parsimony and Maximum Likelihood

As the database of DNA sequences that enables us to study more species grows, the difficulty of building the phylogenetic tree that best describes their evolutionary history also grows. What if you are analyzing data for 50 species? There are 3×10^{76} different ways to arrange 50 species into a tree! And which tree in this huge forest reflects the true phylogeny? Systematists can never be sure of finding the most accurate tree in such a large data set, but they can narrow the possibilities by applying the principles of maximum parsimony and maximum likelihood.

According to the principle of **maximum parsimony**, we should first investigate the simplest explanation that is consistent with the facts. (The parsimony principle is also called "Occam's razor" after William of Occam, a 14th-century English philosopher who advocated solving problems by "shaving away" unnecessary complications.) In the case of trees based on morphology, the most parsimonious tree requires the fewest evolutionary events, as measured by the origin of shared derived morphological

▼ **Figure 26.14 Branch lengths can indicate time.** This tree is based on the same DNA data as that in Figure 26.13, but here the branch points are dated based on fossil evidence. Thus, the branch lengths are proportional to time. Each lineage has the same total length from the base of the tree to the branch tip, indicating that all the lineages have diverged from the common ancestor for equal amounts of time.



characters. For phylogenies based on DNA, the most parsimonious tree requires the fewest base changes.

A **maximum likelihood** approach identifies the tree most likely to have produced a given set of DNA data based on certain probability rules about how DNA sequences change over time. For example, the underlying probability rules could be based on the assumption that all nucleotide substitutions are equally likely. If evidence suggests that this assumption is not correct, more complex rules could be devised to account for different rates of change among different nucleotides or at different positions in a gene.

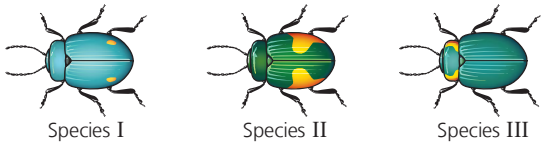
Scientists have developed many computer programs to search for trees that are parsimonious and likely. When a large amount of accurate data is available, the methods used in these programs usually yield similar trees. As an example of one method, **Figure 26.15** walks you through the process of identifying the most parsimonious molecular tree for a three-species problem. Computer programs use the

▼ Figure 26.15 Research Method

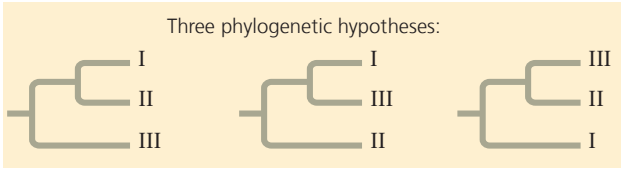
Applying Parsimony to a Problem in Molecular Systematics

Application In considering possible phylogenies for a group of species, systematists compare molecular data for the species. An efficient way to begin is by identifying the most parsimonious hypothesis—the one that requires the fewest evolutionary events (molecular changes) to have occurred.

Technique Follow the numbered steps as we apply the principle of parsimony to a hypothetical phylogenetic problem involving three closely related beetle species.



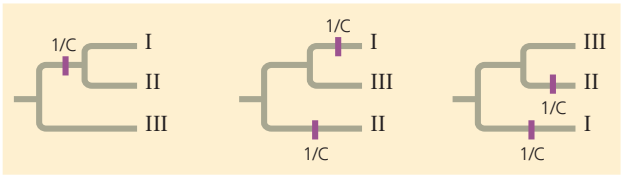
1 First, draw the three possible trees for the species. (Although only three trees are possible when ordering three species, the number of possible trees increases rapidly with the number of species: There are 15 trees for four species and 34,459,425 trees for 10 species.)



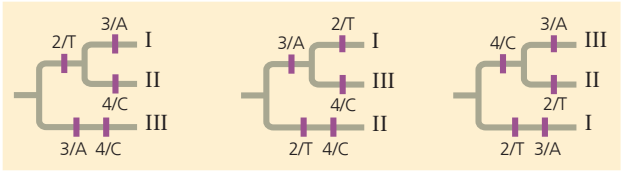
2 Tabulate the molecular data for the species. In this simplified example, the data represent a DNA sequence consisting of just four nucleotide bases. Data from several outgroup species (not shown) were used to infer the ancestral DNA sequence.

	Site 1	2	3	4
Species I	C	T	A	T
Species II	C	T	T	C
Species III	A	G	A	C
Ancestral sequence	A	G	T	T

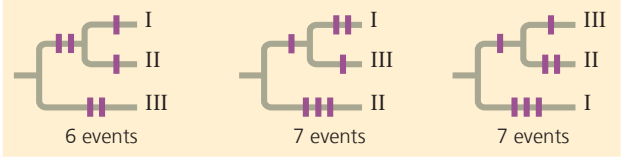
3 Now focus on site 1 in the DNA sequence. In the tree on the left, a single base-change event, represented by the purple hatch mark on the branch leading to species I and II (and labeled 1/C, indicating a change at site 1 to nucleotide C), is sufficient to account for the site 1 data. In the other two trees, two base-change events are necessary.



4 Continuing the comparison of bases at sites 2, 3, and 4 reveals that each of the three trees requires a total of five additional base-change events (purple hatch marks).



Results To identify the most parsimonious tree, we total all of the base-change events noted in steps 3 and 4. We conclude that the first tree is the most parsimonious of the three possible phylogenies. (In a real example, many more sites would be analyzed. Hence, the trees would often differ by more than one base-change event.)



principle of parsimony to estimate phylogenies in a similar way: They examine large numbers of possible trees and identify those that require the fewest evolutionary changes.

Phylogenetic Trees as Hypotheses

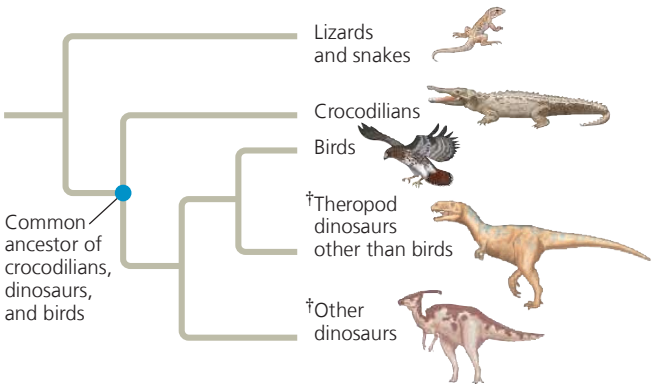
This is a good place to reiterate that any phylogenetic tree represents a hypothesis about how the organisms in the tree are related to one another. The best hypothesis is the one that best fits all the available data. A phylogenetic hypothesis may be modified when new evidence compels systematists to revise their trees. Indeed, while many older phylogenetic hypotheses have been supported by new morphological and molecular data, others have been changed or rejected.

Thinking of phylogenies as hypotheses also allows us to use them in a powerful way: We can make and test predictions based on the assumption that a particular phylogeny—our hypothesis—is correct. For example, in an approach known as *phylogenetic bracketing*, we can predict (by parsimony) that features shared by two groups of closely related organisms are present in their common ancestor and all of its descendants unless independent data indicate otherwise. (Note that "prediction" can refer to unknown past events as well as to evolutionary changes yet to occur.)

This approach has been used to make novel predictions about dinosaurs. For example, there is evidence that birds descended from the theropods, a group of bipedal dinosaurs. As seen in **Figure 26.16**, the closest living relatives of birds are crocodiles. Birds and crocodiles share numerous features: They have four-chambered hearts, they "sing" to defend territories and attract mates (although a crocodile's "song" is more like a bellow), and they build nests. Both birds and crocodiles also care for their eggs by warming them. Birds warm their eggs by sitting on them, whereas crocodiles cover their eggs with their neck. Reasoning that any feature shared by birds and crocodiles is likely to have been present in their common ancestor (denoted by the blue dot in Figure 26.16) and *all* of its descendants, biologists predicted that dinosaurs had four-chambered hearts, sang, built nests, and cared for their eggs.

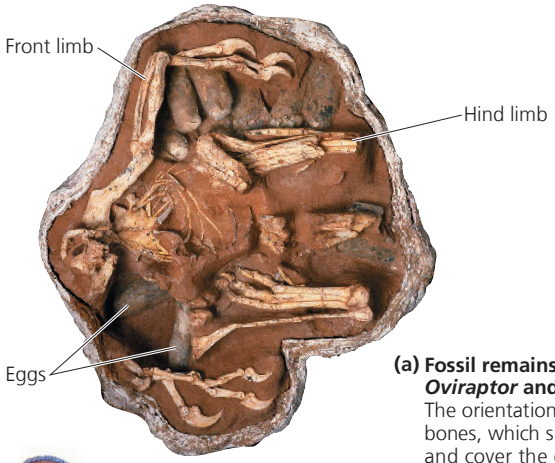
Internal organs, such as the heart, rarely fossilize, and it is, of course, difficult to test whether dinosaurs sang to defend territories and attract mates. However, fossil discoveries have supported the prediction that dinosaurs built nests and cared for their eggs. First, a fossil embryo of an *Oviraptor* dinosaur was found, still inside its egg. This egg was identical to those found in another fossil, one that showed an *Oviraptor* crouching over a group of eggs in a posture similar to how birds sit on their nests today **(Figure 26.17)**. Researchers suggested that the *Oviraptor* dinosaur preserved in this second fossil died while incubating or protecting its eggs. The broader conclusion that emerged from this work—that dinosaurs built nests and cared for their eggs—has since been strengthened by additional fossil discoveries that show that other species

▼ Figure 26.16 A phylogenetic tree of birds and their close relatives. (A dagger, †, indicates extinct lineages.)



VISUAL SKILLS *In this tree diagram, what is the sister taxon of the clade that includes dinosaurs and their most recent common ancestor? Explain.*

▼ Figure 26.17 Fossil support for a phylogenetic prediction: Dinosaurs built nests and cared for their eggs.



(a) Fossil remains of *Oviraptor* and eggs. The orientation of the bones, which surround and cover the eggs, suggests that the dinosaur died while incubating or protecting its eggs.



(b) Artist's reconstruction of the dinosaur's posture on its nest based on the fossil findings.

of dinosaurs built nests and sat on their eggs. Finally, by supporting predictions based on the phylogenetic hypothesis shown in Figure 26.16, fossil discoveries of nests and parental care in dinosaurs provide independent data that suggest that the hypothesis is correct.

CONCEPT CHECK 26.3

1. To distinguish a particular clade of mammals within the larger clade that corresponds to class Mammalia, would hair be a useful character? Why or why not?
2. The most parsimonious tree of evolutionary relationships can be inaccurate. How can this occur?
3. **WHAT IF?** Draw a phylogenetic tree that includes the relationships from Figure 25.7 and Figure 26.16. Traditionally, all the taxa shown besides birds and mammals were classified as reptiles. Would a cladistic approach support that classification? Explain.

For suggested answers, see Appendix A.

CONCEPT 26.4

An organism's evolutionary history is documented in its genome

As you have seen in this chapter, comparisons of nucleic acids or other molecules can be used to deduce relatedness. In some cases, such comparisons can reveal phylogenetic relationships that cannot be determined by nonmolecular methods such as comparative anatomy. For example, the analysis of molecular data helps us uncover evolutionary relationships between groups that have little common ground for morphological comparison, such as animals and fungi. And molecular methods allow us to reconstruct phylogenies among groups of present-day organisms for which the fossil record is poor or lacking entirely.

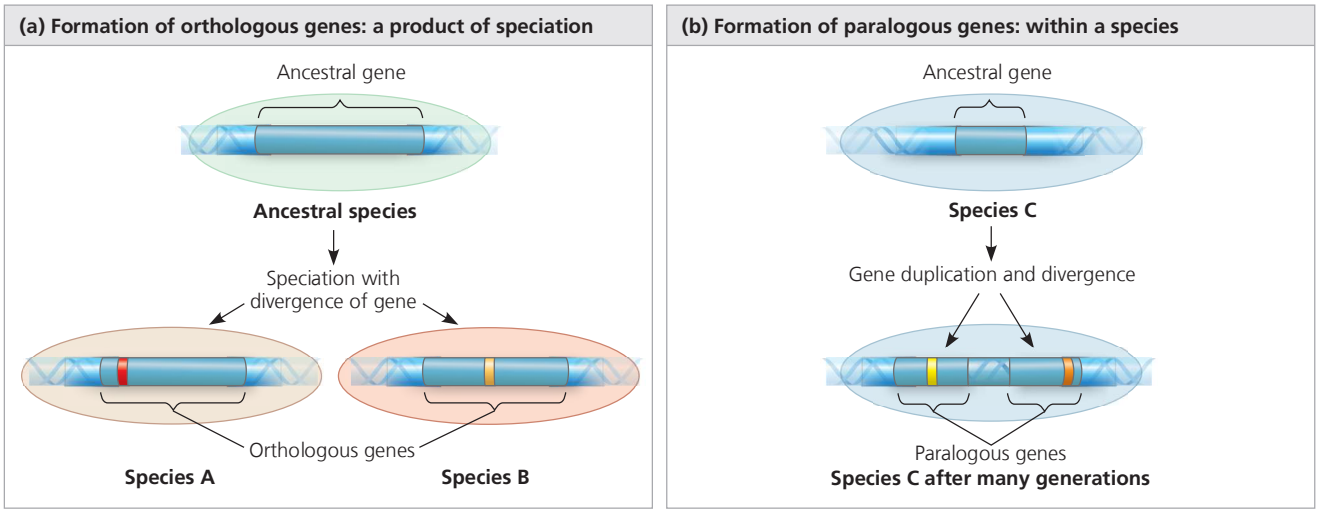
Different genes can evolve at different rates, even in the same evolutionary lineage. As a result, molecular trees can represent short or long periods of time, depending on which genes are used. For example, the DNA that codes for ribosomal RNA (rRNA) changes relatively slowly. Therefore, comparisons of DNA sequences in these genes are useful for investigating relationships between taxa that diverged hundreds of millions of years ago. Studies of rRNA sequences indicate, for instance, that fungi are more closely related to animals than to plants. In contrast, mitochondrial DNA (mtDNA) evolves relatively rapidly and can be used to explore recent evolutionary events. One research team has traced the relationships among Native American groups through their mtDNA sequences. The molecular findings corroborate other evidence that the Pima of Arizona, the Maya of Mexico, and the Yanomami of Venezuela are closely related, probably descending from the first of three waves of immigrants that crossed the Bering Land Bridge from Asia to the Americas about 15,000 years ago.

Gene Duplications and Gene Families

What do molecular data reveal about the evolutionary history of genome change? Consider gene duplication, which can play an important role in evolution because it increases the number of genes in the genome, providing more opportunities for further evolutionary changes. Molecular techniques now allow us to trace the phylogenies of gene duplications. These molecular phylogenies must account for repeated duplications that have resulted in *gene families*, groups of related genes within an organism's genome (see Figure 21.10).

Accounting for such duplications leads us to distinguish two types of homologous genes **(Figure 26.18)**: orthologous genes and paralogous genes. In **orthologous genes** from the Greek *orthos*, exact), the homology is the result of a speciation event

▼ Figure 26.18 Two types of homologous genes. Colored bands mark regions of the genes where differences in base sequences have accumulated.



and hence occurs between genes found in different species (see Figure 26.18a). For example, the genes that code for cytochrome *c* (a protein that functions in electron transport chains) in humans and dogs are orthologous. In **paralogous genes** (from the Greek *para*, in parallel), the homology results from gene duplication; hence, multiple copies of these genes have diverged from one another within a species (see Figure 26.18b). In Concept 23.1, you encountered the example of olfactory receptor genes, which have undergone many gene duplications in vertebrates; humans have 380 functional copies of these paralogous genes, while mice have 1,200.

Note that orthologous genes can only diverge after speciation has taken place, that is, after the genes are found in separate gene pools. Thus, differences among orthologous genes reflect the history of speciation events, making them well-suited for inferring phylogeny. For example, although the cytochrome *c* genes in humans and dogs serve the same function, the gene's sequence in humans has diverged from that in dogs in the time since these species last shared a common ancestor. Paralogous genes, on the other hand, can diverge within a species because they are present in more than one copy in the genome. The paralogous genes that make up the olfactory receptor gene family in humans have diverged from each other during our long evolutionary history. They now specify proteins that confer sensitivity to a wide variety of molecules, ranging from food odors to sex pheromones.

Genome Evolution

Now that we can compare the entire genomes of different organisms, including our own, two patterns have emerged. First, lineages that diverged long ago often share many orthologous genes. For example, though the human and mouse lineages diverged about 65 million years ago, 99% of the genes of humans and mice are orthologous. And 50% of human genes are orthologous with those of yeast, despite 1 billion years of divergent evolution. Such commonalities explain why disparate organisms nevertheless share many biochemical and developmental pathways. As a result of these shared pathways, the functioning of genes linked to diseases in humans can often be investigated by studying yeast and other organisms distantly related to humans.

Second, the number of genes a species has doesn't seem to increase through duplication at the same rate as perceived phenotypic complexity. Humans have only about four times as many genes as yeast, a single-celled eukaryote, even though—unlike yeast—we have a large, complex brain and a body with more than 200 different types of tissues. Evidence is emerging that many human genes are more versatile than those of yeast: A single human gene can encode multiple proteins that perform different tasks in various body tissues. Unraveling the mechanisms that cause this genomic versatility and phenotypic variation is an exciting challenge.

CONCEPT CHECK 26.4

1. Explain how comparing proteins of two species can yield data about the species' evolutionary relationship.
2. Distinguish orthologous from paralogous genes. Which of these two types of genes should be used to infer phylogeny? Explain your answer.
3. **MAKE CONNECTIONS** Review Figure 18.12, then suggest how a particular gene could have different functions in different tissues within an organism.

For suggested answers, see Appendix A.

CONCEPT 26.5

Molecular clocks help track evolutionary time

One goal of evolutionary biology is to understand the relationships among all organisms. It is also helpful to know when lineages diverged from one another, including those for which there is no fossil record. But how can we determine the timing of phylogenies that extend beyond the fossil record?

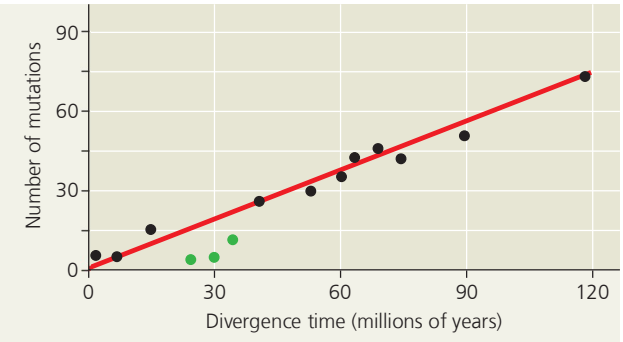
Molecular Clocks

We stated earlier that researchers have estimated that the common ancestor of Hawaiian silversword plants lived about 5 million years ago. How did they make this estimate? They relied on the concept of a **molecular clock**, an approach for measuring the absolute time of evolutionary change based on the observation that some genes and other regions of genomes appear to evolve at constant rates. An assumption underlying the molecular clock is that the number of nucleotide substitutions in orthologous genes is proportional to the time that has elapsed since the genes branched from their common ancestor. In the case of paralogous genes, the number of substitutions is proportional to the time since the ancestral gene was duplicated.

We can calibrate the molecular clock of a gene that has a reliable average rate of evolution by graphing the number of genetic differences—for example, nucleotide, codon, or amino acid differences—against the dates of evolutionary branch points that are known from the fossil record **(Figure 26.19)**. The average rates of genetic change inferred from such graphs can then be used to estimate the dates of events that cannot be discerned from the fossil record, such as the origin of the silverswords discussed earlier.

Of course, no gene marks time with complete precision. In fact, some portions of the genome appear to have evolved in irregular bursts that are not at all clocklike. And even those genes that seem to act as reliable molecular clocks are accurate only in the statistical sense of showing a fairly smooth *average* rate of change. Over time, there may still be deviations from that average rate. Furthermore, the same gene may evolve at

▼ Figure 26.19 A molecular clock for mammals. The number of accumulated mutations in seven well-studied proteins has increased over time in a consistent manner for most mammal species. The three green data points represent primate species, whose proteins appear to have evolved more slowly than those of other mammals. The divergence time for each data point was based on fossil evidence.



INTERPRET THE DATA *Use the graph to estimate the divergence time for a mammal with a total of 30 mutations in the seven proteins.*

different rates in different groups of organisms. Finally, when comparing genes that are clocklike, the rate of the clock may vary greatly from one gene to another; some genes evolve a million times faster than others.

Differences in Clock Speed

What causes such differences in the speed at which clocklike genes evolve? The answer stems from the fact that some mutations are selectively neutral—neither beneficial nor detrimental. Of course, many new mutations are harmful and are removed quickly by selection. But if most of the rest are neutral and have little or no effect on fitness, then the rate of evolution of those neutral mutations should indeed be regular, like a clock. Differences in the clock rate for different genes are related to how important a gene is. If the exact sequence of amino acids that a gene specifies is essential to survival, most of the mutational changes will be harmful and only a few will be neutral. As a result, such genes change only slowly. But if the exact sequence of amino acids is less critical, fewer of the new mutations will be harmful and more will be neutral. Such genes change more quickly.

Potential Problems with Molecular Clocks

As we've seen, molecular clocks do not run as smoothly as would be expected if the underlying mutations were selectively neutral. Many irregularities are likely to be the result of natural selection in which certain DNA changes are favored over others. Indeed, evidence suggests that almost half the amino acid differences in proteins of two *Drosophila* species, *D. simulans* and *D. yakuba*, are not neutral but have resulted from natural selection. But because the direction of natural selection may change repeatedly over long periods of time (and hence may average out), some genes experiencing selection can nevertheless serve as approximate markers of elapsed time.

Another question arises when researchers attempt to extend molecular clocks beyond the time span documented by the fossil record. Although an abundant fossil record extends back only about 550 million years, molecular clocks have been used to date evolutionary divergences that occurred a billion or more years ago. These estimates assume that the clocks have been constant for all that time. Such estimates are highly uncertain.

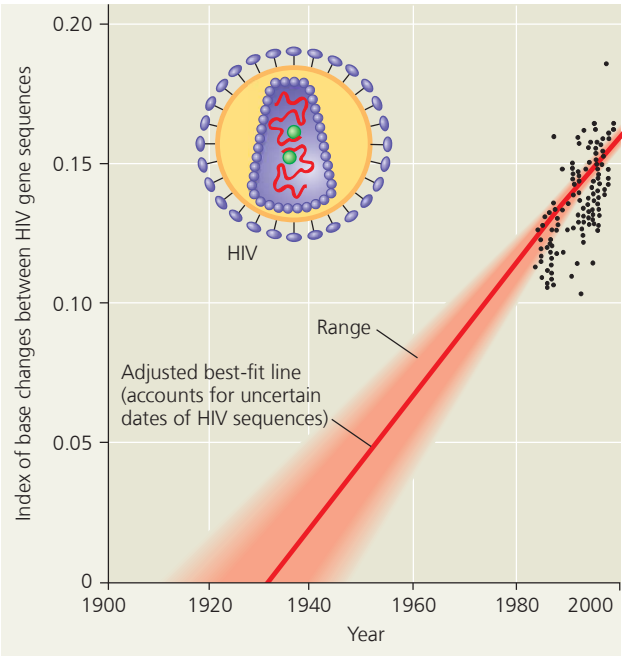
In some cases, problems may be avoided by calibrating molecular clocks with data on the rates at which genes have evolved in different taxa. In other cases, problems may be avoided by using many genes rather than just using one or a few genes. By using many genes, fluctuations in evolutionary rate due to natural selection or other factors that vary over time may average out. For example, one group of researchers constructed molecular clocks of vertebrate evolution from published sequence data for 658 nuclear genes. Despite the broad period of time covered (nearly 600 million years) and the fact that natural selection probably affected some of these genes, their estimates of divergence times agreed closely with fossil-based estimates. As this example suggests, if used with care, molecular clocks can aid our understanding of evolutionary relationships.

Applying a Molecular Clock: Dating the Origin of HIV

Researchers have used a molecular clock to date the origin of HIV infection in humans. Phylogenetic analysis shows that HIV, the virus that causes AIDS, is descended from viruses that infect chimpanzees and other primates. (Most of these viruses do not cause AIDS-like diseases in their native hosts.) When did HIV jump to humans? There is no simple answer because the virus has spread to humans more than once. The multiple origins of HIV are reflected in the variety of strains (genetic types) of the virus. HIV's genetic material is made of RNA, and like other RNA viruses, it evolves quickly.

The most widespread strain in humans is HIV-1 M. To pinpoint the earliest HIV-1 M infection, researchers compared samples of the virus from various times during the epidemic, including a sample from 1959. Comparisons of gene sequences showed that the virus has evolved in a clocklike fashion. Extrapolating backward in time using the molecular clock indicates that the HIV-1 M strain first spread to humans around 1930 **(Figure 26.20)**. A later study, which dated the origin of HIV using a more advanced molecular clock approach than that covered in this book, estimated that the HIV-1 M strain first spread to humans around 1910.

▼ **Figure 26.20 Dating the origin of HIV-1 M.** The black data points are based on DNA sequences of an HIV gene in patients' blood samples. (The dates when these individual HIV gene sequences arose are not certain because a person can harbor the virus for years before symptoms occur.) Projecting the gene's rate of change backward in time by this method suggests that the virus originated in the 1930s.



CONCEPT CHECK 26.5

1. What is a molecular clock? What assumption underlies the use of a molecular clock?
2. **MAKE CONNECTIONS** Review Concept 17.5. Then explain how numerous base changes could occur in an organism's DNA yet have no effect on its fitness.

For suggested answers, see Appendix A.

CONCEPT 26.6

Our understanding of the tree of life continues to change based on new data

The discovery that the glass lizard in Figure 26.1 evolved from a different lineage of legless lizards than did snakes is one example of how our understanding of life's diversity is informed by systematics. Indeed, in recent decades, systematists have gained insight into even the very deepest branches of the tree of life by analyzing DNA sequence data.

From Two Kingdoms to Three Domains

Biologists once classified all known species into two kingdoms: plants and animals. Classification schemes with more than two kingdoms gained broad acceptance in the late 1960s, when many biologists recognized five kingdoms: Monera (prokaryotes), Protista (a diverse kingdom consisting mostly of unicellular organisms), Plantae, Fungi, and Animalia. This system highlighted the two fundamentally different types of cells, prokaryotic and eukaryotic, and set the prokaryotes apart from all eukaryotes by placing them in their own kingdom, Monera.

However, phylogenies based on genetic data soon revealed a problem with this system: Some prokaryotes differ as much from each other as they do from eukaryotes. Such difficulties led biologists to adopt a three-domain system. The three domains—Bacteria, Archaea, and Eukarya—are a classification level higher than the kingdom level. The validity of these domains has been supported by many studies, including a recent study that analyzed nearly 100 completely sequenced genomes.

The domain Bacteria contains most of the currently known prokaryotes, while the domain Archaea consists of a diverse group of prokaryotic organisms that inhabit a wide variety of environments. The domain Eukarya consists of all the organisms that have cells containing true nuclei. This domain includes many groups of single-celled organisms as well as multicellular plants, fungi, and animals. **Figure 26.21** represents one possible phylogenetic tree for the three domains and some of the many lineages they encompass.

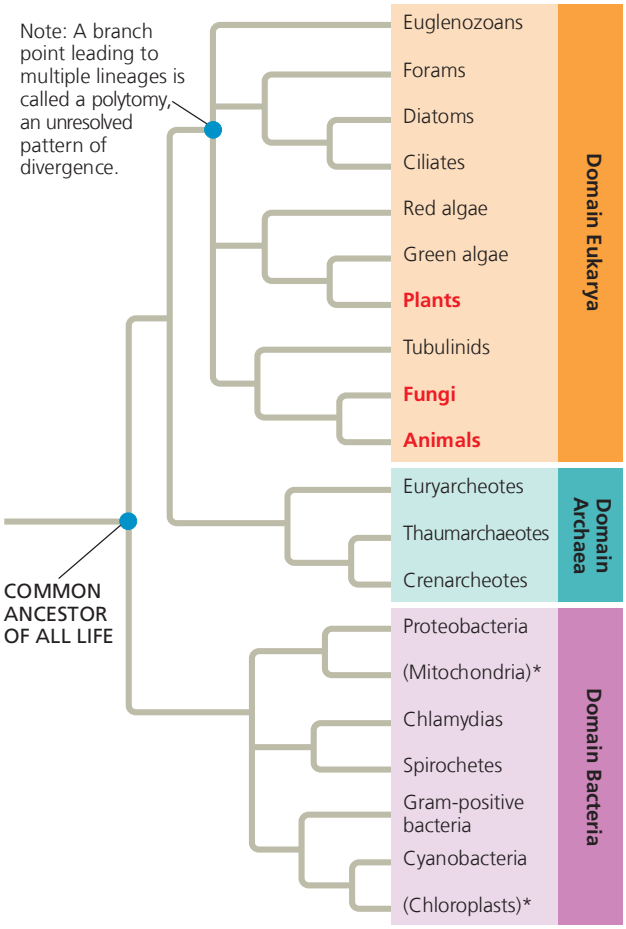
The three-domain system highlights the fact that much of the history of life has been about single-celled organisms. The two prokaryotic domains consist entirely of single-celled organisms, and even in Eukarya, only the branches labeled in red type (plants, fungi, and animals) are dominated by multicellular organisms. Of the five kingdoms previously recognized by systematists, most biologists continue to recognize Plantae, Fungi, and Animalia, but not Monera and Protista. The kingdom Monera is obsolete because it would have members in two different domains. The kingdom Protista has also crumbled because it includes members that are more closely related to plants, fungi, or animals than to other protists (see Figure 28.5).

New research continues to change our understanding of the tree of life. For example, recent metagenomic studies have uncovered the genomes of many new species of archaea, leading to discovery of the Thaumarchaeota and other previously unknown phyla of archaea. One of these newly discovered groups, the lokiarcheaota, may represent the long-sought-after sister group of the eukaryotes. If confirmed, this discovery could help shed light on how eukaryotes arose from their prokaryotic ancestors (see Concepts 27.4 and 28.1).

The Important Role of Horizontal Gene Transfer

In the phylogeny shown in Figure 26.21, the first major split in the history of life occurred when bacteria diverged from other organisms. If this tree is correct, eukaryotes and archaea are more closely related to each other than either is to bacteria.

▼ Figure 26.21 The three domains of life. This phylogenetic tree is based on sequence data for rRNA and other genes. For simplicity, only some of the major branches in each domain are shown. Lineages within Eukarya that are dominated by multicellular organisms (plants, fungi, and animals) are in red type, while the two lineages denoted by an asterisk are based on DNA from cellular organelles. All other lineages consist solely or mainly of single-celled organisms.



MAKE CONNECTIONS *After reviewing endosymbiont theory (see Figure 6.16), explain the specific positions of the mitochondrion and chloroplast lineages on this tree.*

This reconstruction of the tree of life is based in part on sequence comparisons of rRNA genes, which code for the RNA components of ribosomes. However, some other genes reveal a different set of relationships. For example, researchers have found that many of the genes that influence metabolism in yeast (a unicellular eukaryote) are more similar to genes in the domain Bacteria than they are to genes in the domain Archaea—a finding that suggests that the eukaryotes may share a more recent common ancestor with bacteria than with archaea.

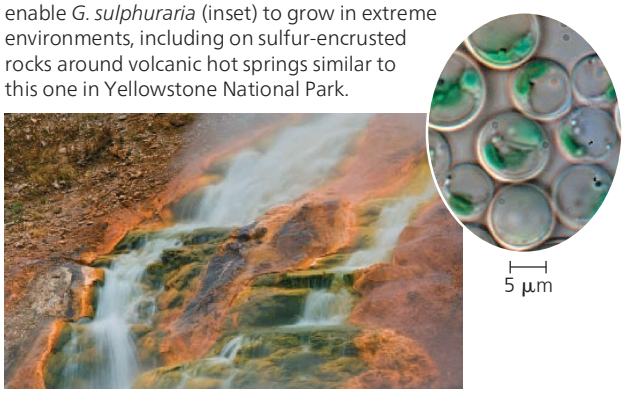
What causes trees based on data from different genes to yield such different results? Comparisons of complete genomes from the three domains show that there have been substantial movements of genes between organisms in the different domains. These took place through **horizontal gene transfer**, a process in which genes are transferred from one genome to another through mechanisms such as exchange of transposable elements and plasmids, viral infection (see Concept 19.2), and fusions of organisms (as when a host and its endosymbiont become a single organism). Recent research reinforces the view that horizontal gene transfer is important. For example, one study found that on average, 80% of the genes in 181 prokaryotic genomes had moved between species at some point during the course of evolution. Because phylogenetic trees are based on the assumption that genes are passed vertically from one generation to the next, the occurrence of such horizontal transfer events helps to explain why trees built using different genes can give inconsistent results.

Horizontal gene transfer can also occur between eukaryotes. For example, over 200 cases of the horizontal transfer of transposons have been reported in eukaryotes, including humans and other primates, plants, birds, and lizards. Nuclear genes have also been transferred horizontally from one eukaryote to another. The **Scientific Skills Exercise** describes one such example, giving you the opportunity to interpret data on the transfer of a pigment gene to an aphid from another species.

Studies show that eukaryotes can even acquire genes by horizontal gene transfer from prokaryotes. For example, a recent genomic analysis showed that the alga *Galdieria sulphuraria* **(Figure 26.22)** acquired about 5% of its nuclear genes from various bacterial and archaeal species. Unlike most eukaryotes, this alga can survive in environments that are highly acidic or extremely hot, as well as those with high concentrations of heavy metals. The researchers identified specific genes transferred from prokaryotes that have enabled *G. sulphuraria* to thrive in such extreme habitats.

Overall, horizontal gene transfer has played a key role throughout the evolutionary history of life, and it continues to occur today. Some biologists have argued that horizontal gene transfer was so common that the early history of life should be represented not as a dichotomously branching tree like that in Figure 26.21, but rather as a tangled network of

▼ Figure 26.22 A recipient of transferred genes: the alga *Galdieria sulphuraria*. Genes received from prokaryotes enable *G. sulphuraria* (inset) to grow in extreme environments, including on sulfur-encrusted rocks around volcanic hot springs similar to this one in Yellowstone National Park.



Scientific Skills Exercise

Using Protein Sequence Data to Test an Evolutionary Hypothesis

Did Aphids Acquire Their Ability to Make Carotenoids Through Horizontal Gene Transfer? Carotenoids are colored molecules that have diverse functions in many organisms, such as photosynthesis in plants and light detection in animals. Plants and many microorganisms can synthesize carotenoids from scratch, but animals generally cannot (they must obtain carotenoids from their diet). One exception is the pea aphid *Acyrthosiphon pisum*, a small, plant-dwelling insect whose genome includes a full set of genes for the enzymes needed to make carotenoids. Because other animals lack these genes, it is unlikely that aphids inherited them from a single-celled common ancestor shared with microorganisms and plants. So where did they come from? Evolutionary biologists hypothesized that an aphid ancestor acquired these genes by horizontal gene transfer from distantly related organisms.

How the Experiment Was Done Scientists obtained the DNA sequences for the carotenoid-biosynthesis genes from several species, including aphids, fungi, bacteria, and plants. A computer "translated" these sequences into amino acid sequences of the encoded polypeptides and aligned the amino acid sequences. This allowed the team to compare the corresponding polypeptides in the different organisms.

Data from the Experiment The sequences below show the first 60 amino acids of one polypeptide of the carotenoid-biosynthesis enzymes in the plant *Arabidopsis thaliana* (bottom) and the corresponding amino acids in five nonplant species, using the one-letter abbreviations for the amino acids (see Figure 5.14). A dash (–) indicates a gap inserted in a sequence to optimize its alignment with the corresponding sequence in *Arabidopsis*.



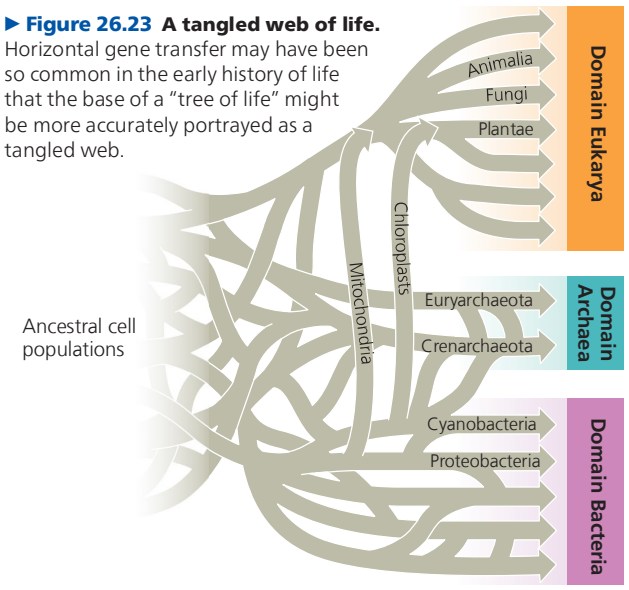
INTERPRET THE DATA

1. In the rows of data for the organisms being compared with the aphid, highlight the amino acids that are identical to the corresponding amino acids in the aphid.
2. Which organism has the most amino acids in common with the aphid? Rank the partial polypeptides from the other four organisms in degree of similarity to that of the aphid.
3. **(a)** Do these data support the hypothesis that aphids acquired the gene for this polypeptide by horizontal gene transfer? Why or why not? **(b)** If horizontal gene transfer did occur, what type of organism is likely to have been the source?
4. What additional sequence data would support your hypothesis?
5. How would you account for the similarities between the aphid sequence and the sequences for the bacteria and plant?

Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

Data from Nancy A. Moran, Yale University. See N. A. Moran and T. Jarvik, Lateral transfer of genes from fungi underlies carotenoid production in aphids, *Science* 328:624–627 (2010).

Organism	Alignment of Amino Acid Sequences					
Acyrthosiphon (aphid)	IKIIIIGSGV	GGTAAAARLS	KKGFQVEVYE	KNSYNGGRCS	IIR-HNGHRF	DQGPSL––YL
Ustilago (fungus)	KKVVIIGAGA	GGTALAARLG	RRGYSVTVLE	KNSFGGGRCS	LIH-HDGHRW	DQGPSL––YL
Gibberella (fungus)	KSVIVIGAGV	GGVSTAARLA	KAGFKVTILE	KNDFTGGRCS	LIH-NDGHRF	DQGPSL––LL
Staphylococcus (bacterium)	MKIAVIGAGV	TGLAAAARIA	SQGHEVTIFE	KNNNVGGRMN	QLK-KDGFTF	DMGPTI––VM
Pantoea (bacterium)	KRTFVIGAGF	GGLALAIRLQ	AAGIATTVLE	QHDKPGGRAY	VWQ-DQGFTF	DAGPTV––IT
Arabidopsis (plant)	WDAVVIGGGH	NGLTAAAYLA	RGGLSVAVLE	RRHVIGGAAV	TEEIVPGFKF	SRCSYLQGLL



▶ Figure 26.23 A tangled web of life. Horizontal gene transfer may have been so common in the early history of life that the base of a "tree of life" might be more accurately portrayed as a tangled web.

connected branches **(Figure 26.23)**. Although scientists continue to debate how best to portray the earliest steps in the history of life, in recent decades there have been many exciting discoveries about evolutionary events that occurred over time. We'll explore such discoveries in the rest of this unit, beginning with Earth's earliest inhabitants, the prokaryotes.

Mastering Biology
Interview with Nancy Moran: Studying symbioses and horizontal gene transfer



CONCEPT CHECK 26.6

1. Why is the kingdom Monera no longer considered a valid taxon?
2. Explain why phylogenies based on different genes can yield different branching patterns for the tree of all life.
3. **MAKE CONNECTIONS** Explain how the origin of eukaryotes is thought to have represented a fusion of organisms, leading to extensive horizontal gene transfer. (See Figure 25.10.)

For suggested answers, see Appendix A.

26 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

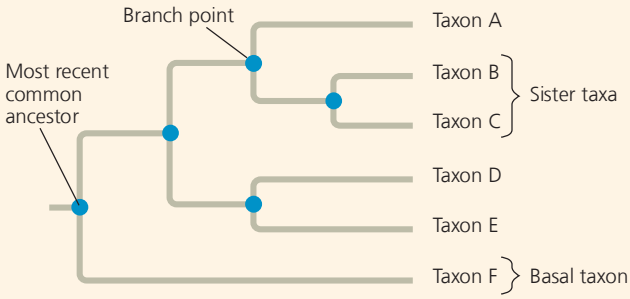
SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

CONCEPT 26.1

Phylogenies show evolutionary relationships *(pp. 554–558)*

- Linnaeus's **binomial** classification system gives organisms two-part names: a **genus** plus a specific epithet.
- In the Linnaean system, species are grouped in increasingly broad **taxa**: Related genera are placed in the same **family**, families in **orders**, orders in **classes**, classes in **phyla**, phyla in **kingdoms**, and (more recently) kingdoms in **domains**.
- Systematists depict evolutionary relationships as branching **phylogenetic trees**. Many systematists propose that classification be based entirely on evolutionary relationships.



- Unless branch lengths are proportional to time or genetic change, a phylogenetic tree indicates only patterns of descent.
- Much information can be learned about a species from its evolutionary history; hence, phylogenies are useful in a wide range of applications.

? *Humans and chimpanzees are sister species. Explain what this statement means.*

CONCEPT 26.2

Phylogenies are inferred from morphological and molecular data *(pp. 558–559)*

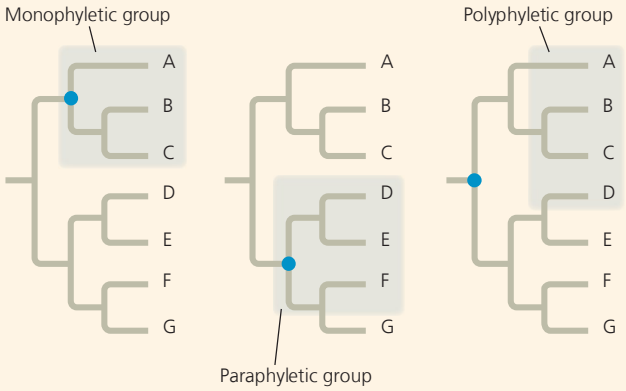
- Organisms with similar morphologies or DNA sequences are likely to be more closely related than organisms with very different structures and genetic sequences.
- To infer phylogeny, **homology** (similarity due to shared ancestry) must be distinguished from **analogy** (similarity due to convergent evolution).
- Computer programs are used to align comparable DNA sequences and to distinguish molecular homologies from coincidental matches between taxa that diverged long ago.

? *Why is it necessary to distinguish homology from analogy to infer phylogeny?*

CONCEPT 26.3

Shared characters are used to construct phylogenetic trees *(pp. 559–565)*

- A **clade** is a monophyletic group that includes an ancestral species and all of its descendants.



- Clades can be distinguished by their **shared derived characters**.
- Among phylogenies, the most parsimonious tree is the one that requires the fewest evolutionary changes. The most likely tree is the one based on the most likely pattern of changes.
- Well-supported phylogenetic hypotheses are consistent with a wide range of data.

? *Explain the logic of using shared derived characters to infer phylogeny.*

CONCEPT 26.4

An organism's evolutionary history is documented in its genome *(pp. 565–566)*

- **Orthologous genes** are homologous genes found in different species as a result of speciation. **Paralogous genes** are homologous genes within a species that result from gene duplication; such genes can diverge and potentially take on new functions.
- Distantly related species often have many orthologous genes. The small variation in gene number in organisms of varying complexity suggests that genes are versatile and may have multiple functions.

? *When reconstructing phylogenies, is it more useful to compare orthologous or paralogous genes? Explain.*

CONCEPT 26.5

Molecular clocks help track evolutionary time *(pp. 566–568)*

- Some regions of DNA change at a rate consistent enough to serve as a **molecular clock**, a method of estimating the date of past evolutionary events based on the amount of genetic change. Other DNA regions change in a less predictable way.
- Molecular clock analyses suggest that the most common strain of HIV jumped from primates to humans in the early 1900s.

? *Describe some assumptions and limitations of molecular clocks.*

CONCEPT 26.6

Our understanding of the tree of life continues to change based on new data *(pp. 568–570)*

- Past classification systems have given way to the current view of the tree of life, which consists of three great domains: Bacteria, Archaea, and Eukarya.

- Phylogenies based in part on rRNA genes suggest that eukaryotes are most closely related to archaea, while data from some other genes suggest a closer relationship to bacteria.
- Genetic analyses indicate that extensive **horizontal gene transfer** has occurred throughout the evolutionary history of life.

? *Why was the five-kingdom system abandoned for a three-domain system?*

TEST YOUR UNDERSTANDING

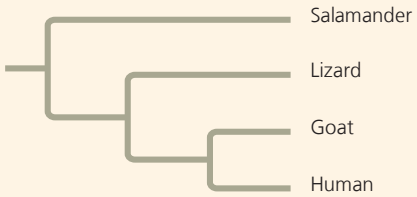
For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

1. In a comparison of birds and mammals, the condition of having four limbs is
   (A) a shared ancestral character.
   (B) a shared derived character.
   (C) a character useful for distinguishing birds from mammals.
   (D) an example of analogy rather than homology.
2. To apply parsimony to constructing a phylogenetic tree,
   (A) choose the tree that assumes all evolutionary changes are equally probable.
   (B) choose the tree in which the branch points are based on as many shared derived characters as possible.
   (C) choose the tree that represents the fewest evolutionary changes, in either DNA sequences or morphology.
   (D) choose the tree with the fewest branch points.

Levels 3-4: Applying/Analyzing

3. **VISUAL SKILLS** In Figure 26.4, which similarly inclusive taxon is represented as descending from the same common ancestor as Canidae?
   (A) Felidae (C) Carnivora
   (B) Mustelidae (D) *Lutra*
4. Three living species X, Y, and Z share a common ancestor T, as do extinct species U and V. A grouping that consists of species T, X, Y, and Z (but not U or V) makes up
   (A) a monophyletic taxon.
   (B) an ingroup, with species U as the outgroup.
   (C) a paraphyletic group.
   (D) a polyphyletic group.
5. **VISUAL SKILLS** Based on the tree below, which statement is correct?



   (A) Lizards and goats form a sister group.
   (B) Salamanders are a sister group to the group containing lizards, goats, and humans.
   (C) Salamanders are more closely related to lizards than to humans.
   (D) Goats and humans are the only sister group shown in this tree.
6. If you were using cladistics to build a phylogenetic tree of cats, which of the following would be the best outgroup?
   (A) wolf (C) lion
   (B) domestic cat (D) leopard
7. **VISUAL SKILLS** The relative lengths of the frog and mouse branches in the phylogenetic tree in Figure 26.13 indicate that
   (A) frogs evolved before mice.
   (B) mice evolved before frogs.
   (C) the homolog evolved more rapidly in the mouse lineage.
   (D) the homolog evolved more slowly in the mouse lineage.

Levels 5-6: Evaluating/Creating

8. **EVOLUTION CONNECTION** Darwin suggested looking at a species' close relatives to learn what its ancestors may have been like. Explain how his suggestion anticipates recent methods, such as phylogenetic bracketing and the use of outgroups in cladistic analysis.
9. **SCIENTIFIC INQUIRY • DRAW IT** (a) Draw a phylogenetic tree based on the characters in the table below. Draw hatch marks on the tree to indicate the origin of characters 1–6. (b) Assume that tuna and dolphins are sister species and redraw the phylogenetic tree accordingly. Use hatch marks to indicate the origin of characters 1–6. (c) Determine how many evolutionary changes are required in each tree. Identify the most parsimonious tree.

Character	Lancelet (outgroup)	Lamprey	Tuna	Salamander	Turtle	Leopard	Dolphin
(1) Backbone	0	1	1	1	1	1	1
(2) Hinged jaw	0	0	1	1	1	1	1
(3) Four limbs	0	0	0	1	1	1	1*
(4) Amnion	0	0	0	0	1	1	1
(5) Milk	0	0	0	0	0	1	1
(6) Dorsal fin	0	0	1	0	0	0	1

*Although adult dolphins have only two obvious limbs (their flippers), as embryos they have two hind-limb buds, for a total of four limbs.

10. **WRITE ABOUT A THEME: INFORMATION** In a short essay (100–150 words), explain how genetic information—along with an understanding of the process of descent with modification—enables scientists to reconstruct phylogenies that extend hundreds of millions of years back in time.
11. **SYNTHESIZE YOUR KNOWLEDGE**



This West Indian manatee (*Trichechus manatus*) is an aquatic mammal. Like amphibians and reptiles, mammals are tetrapods (vertebrates with four limbs). Explain why manatees are considered tetrapods even though they lack hind limbs, and suggest traits that manatees likely share with leopards and other mammals (see Figure 26.12b). Discuss how early members of the manatee lineage might have differed from today's manatees.

For selected answers, see Appendix A.

27 Bacteria and Archaea

KEY CONCEPTS

27.1 Structural and functional adaptations contribute to prokaryotic success *p. 574*

27.2 Rapid reproduction, mutation, and genetic recombination promote genetic diversity in prokaryotes *p. 578*

27.3 Diverse nutritional and metabolic adaptations have evolved in prokaryotes *p. 581*

27.4 Prokaryotes have radiated into a diverse set of lineages *p. 583*

27.5 Prokaryotes play crucial roles in the biosphere *p. 586*

27.6 Prokaryotes have both beneficial and harmful impacts on humans *p. 587*

Study Tip

Make a table: As you read the chapter, identify examples of challenging environments in which prokaryotes thrive. List the structural, metabolic, or other features of prokaryotes that contribute to their success in each of these environments.

Environmental challenge	Prokaryotic feature enabling success
Lack of water	Capsule or slime layer
Exposure to antibiotics	

Go to Mastering Biology

For Students (in eText and Study Area)
- Get Ready for Chapter 27
- Figure 27.13 Walkthrough: Conjugation and Recombination in *E. coli*
- Animation: Structure and Reproduction of Bacteria

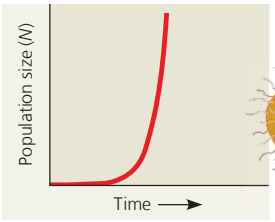
For Instructors to Assign (in Item Library)
- Scientific Skills Exercise: Calculating and Interpreting Means and Standard Errors
- Tutorial: Genetic Transfer in Bacteria



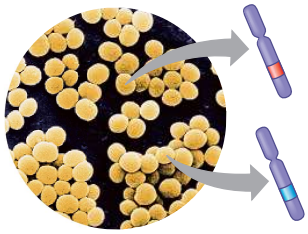
Figure 27.1 The pink color of this lake in Spain is a sign that its waters are much saltier than seawater. Its color is caused not by minerals or other nonliving sources, but by trillions of prokaryotes that thrive in salinities that kill other cells. Other prokaryotes live in environments that are far too cold or hot or acidic for most other organisms.

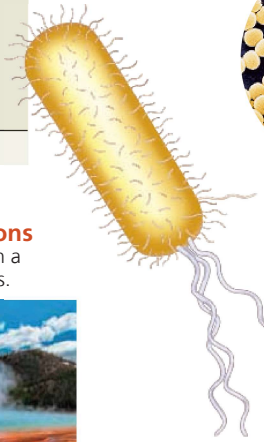
What characteristics enable prokaryotes to reach huge population sizes and thrive in diverse environments?

Due to the organisms' **small size** and **rapid reproduction**, prokaryotic populations can reach enormous numbers.



Because prokaryotic populations are so large, **mutations** produce high genetic diversity, enabling rapid evolution.

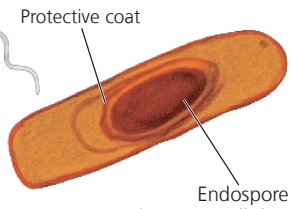




Their **diverse adaptations** enable prokaryotes to live in a wide range of environments.



Rapid evolution in prokaryotic populations results in diverse metabolic and structural adaptations.



Prokaryotes, the single-celled organisms that make up domains Bacteria and Archaea, can thrive in a wide range of extreme environments. Prokaryotic species are also very well adapted to more "normal" habitats—the lands and waters in which most other species are found. Their ability to adapt to a broad range of habitats helps explain why prokaryotes are the most abundant organisms on Earth. Indeed, the number of prokaryotes in a handful of fertile soil is greater than the number of people who have ever lived. In this chapter, we'll examine the adaptations, diversity, and enormous ecological impact of these remarkable organisms.

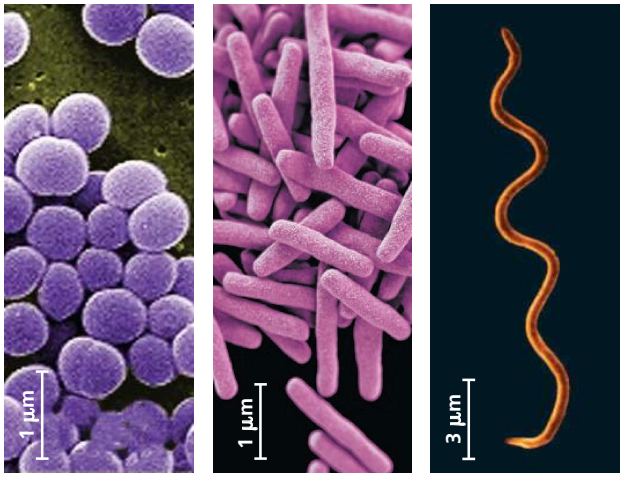
CONCEPT 27.1

Structural and functional adaptations contribute to prokaryotic success

The first organisms to inhabit Earth were prokaryotes that lived 3.5 billion years ago (see Concept 25.3). Throughout their long evolutionary history, prokaryotic populations have been (and continue to be) subjected to natural selection in all kinds of environments, resulting in their enormous diversity today.

We'll begin by describing prokaryotes. Most prokaryotes are unicellular, although the cells of some species remain attached to each other after cell division. Prokaryotic cells typically have diameters of 0.5–5 µm, much smaller than the 10- to 100-µm diameter of many eukaryotic cells. (One notable exception, *Thiomargarita namibiensis*, can be as large as 750 µm in diameter—bigger than a poppy seed.) Prokaryotic cells have a variety of shapes **(Figure 27.2)**.

▼ Figure 27.2 The most common shapes of prokaryotes. **(a)** Cocci (singular, *coccus*) are spherical prokaryotes. They can occur singly, in chains of two or more cells, and in clusters resembling bunches of grapes. **(b)** Bacilli (singular, *bacillus*) are rod-shaped prokaryotes. They are usually solitary, but in some forms the rods are arranged in chains. **(c)** Spiral prokaryotes include spirochetes (shown here), which are corkscrew-shaped; other spiral prokaryotes resemble commas or loose coils (colorized SEMs).



(a) Spherical (b) Rod-shaped (c) Spiral

Finally, although they are unicellular and small, prokaryotes are well organized, achieving all of an organism's life functions within a single cell.

Cell-Surface Structures

A key feature of nearly all prokaryotic cells is the cell wall, which maintains cell shape, protects the cell, and prevents it from bursting in a hypotonic environment (see Figure 7.13). In a hypertonic environment, most prokaryotes lose water and shrink away from their wall. Such water losses can inhibit cell reproduction. Thus, salt can be used to preserve foods because it causes food-spoiling prokaryotes to lose water, preventing them from reproducing rapidly.

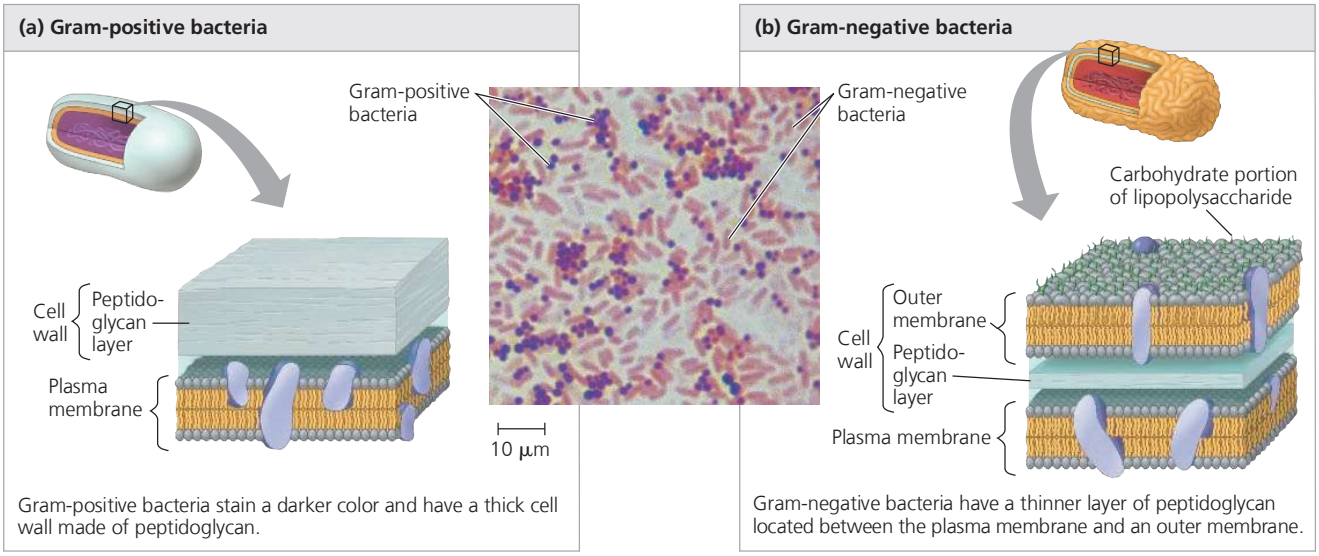
The cell walls of prokaryotes differ in structure from those of eukaryotes. In eukaryotes that have cell walls, such as plants and fungi, the walls are usually made of cellulose or chitin (see Concept 5.2). In contrast, most bacterial cell walls contain **peptidoglycan**, a polymer composed of modified sugars cross-linked by short polypeptides. This molecular fabric encloses the entire bacterium and anchors other molecules that extend from its surface. Archaeal cell walls contain a variety of polysaccharides and proteins but lack peptidoglycan.

Using a technique called the **Gram stain**, developed by the 19th-century Danish physician Hans Christian Gram, scientists can categorize many bacterial species according to differences in cell wall composition. To do this, samples are first stained with crystal violet dye and iodine, then rinsed in alcohol, and finally stained with the red dye safranin, which enters the cell and binds to its DNA. The structure of a bacterium's cell wall determines the staining response **(Figure 27.3)**. **Gram-positive** bacteria have relatively simple walls composed of a thick layer of peptidoglycan. The walls of **gram-negative** bacteria have less peptidoglycan and are structurally more complex, with an outer membrane that contains lipopolysaccharides (carbohydrates bonded to lipids).

Gram staining is a valuable tool in medicine for quickly determining if a patient's infection is due to gram-negative or to gram-positive bacteria. This information has treatment implications. The lipid portions of the lipopolysaccharides in the walls of many gram-negative bacteria are toxic, causing fever or shock. Furthermore, the outer membrane of a gram-negative bacterium helps protect it from the body's defenses. Gram-negative bacteria also tend to be more resistant than gram-positive species to antibiotics because the outer membrane impedes the entry of some drugs. However, some gram-positive species have virulent strains that are resistant to one or more antibiotics. (Figure 22.14 discusses one example: methicillin-resistant *Staphylococcus aureus*, or MRSA, which can cause lethal skin infections.)

The effectiveness of certain antibiotics, such as penicillin, derives from their inhibition of peptidoglycan cross-linking. The resulting cell wall may not be functional, particularly in

▼ Figure 27.3 Gram staining.



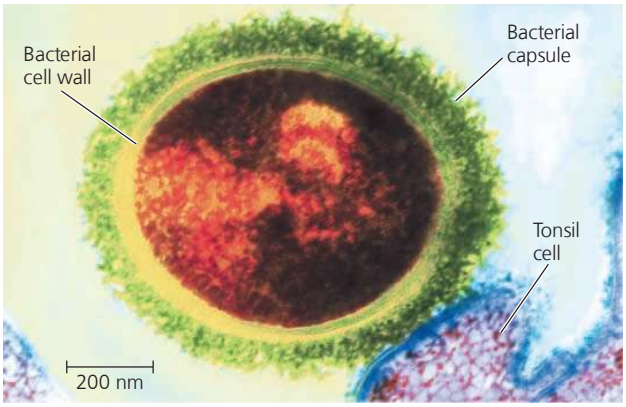
gram-positive bacteria. Such drugs destroy many species of pathogenic bacteria without adversely affecting human cells, which do not have peptidoglycan.

The cell wall of many prokaryotes is surrounded by a sticky layer of polysaccharide or protein. This layer is called a **capsule** if it is dense and well-defined **(Figure 27.4)** or a *slime layer* if it is not as well organized. Both kinds of sticky outer layers enable prokaryotes to adhere to their substrate or to other individuals in a colony. Capsules and slime layers also protect against dehydration, and some capsules shield pathogenic prokaryotes from attacks by their host's immune system.

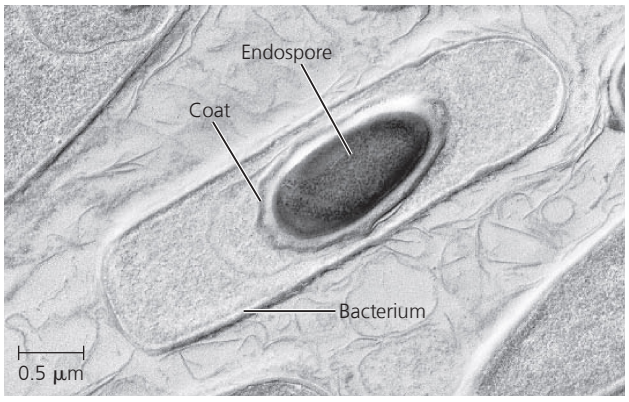
In another way of withstanding harsh conditions, certain bacteria develop resistant cells called **endospores** when they lack water or essential nutrients **(Figure 27.5)**. The original cell produces a copy of its chromosome and surrounds that copy with a multilayered structure, forming the endospore. Water is removed from the endospore, and its metabolism halts. The original cell then lyses, releasing the endospore. Most endospores are so durable that they can survive in boiling water; killing them requires heating lab equipment to 121°C under high pressure. In less hostile environments, endospores can remain dormant but viable for centuries, able to rehydrate and resume metabolism when their environment improves.

Finally, some prokaryotes stick to their substrate or to one another by means of hairlike appendages called **fimbriae**

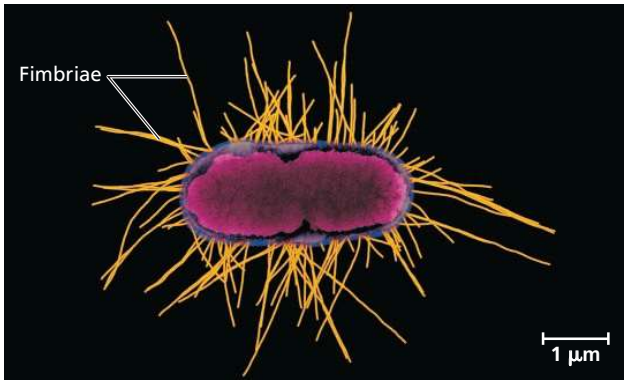
▼ Figure 27.4 Capsule. The polysaccharide capsule around this *Streptococcus* bacterium enables the prokaryote to attach to cells in the respiratory tract—in this colorized TEM, a tonsil cell.



▼ Figure 27.5 An endospore. *Bacillus anthracis*, the bacterium that causes the disease anthrax, produces endospores (TEM). An endospore's protective, multilayered coat helps it survive in the soil for years.



▼ **Figure 27.6** **Fimbriae.** These numerous protein-containing appendages enable some prokaryotes to attach to surfaces or to other cells (colorized TEM).



(singular, *fimbria*) **(Figure 27.6)**. For example, the bacterium that causes gonorrhea, *Neisseria gonorrhoeae*, uses fimbriae to fasten itself to the mucous membranes of its host. Fimbriae are usually shorter and more numerous than **pili** (singular, *pilus*), appendages that pull two cells together prior to DNA transfer from one cell to the other (see Figure 27.12); pili are sometimes referred to as *sex pili*.

Motility

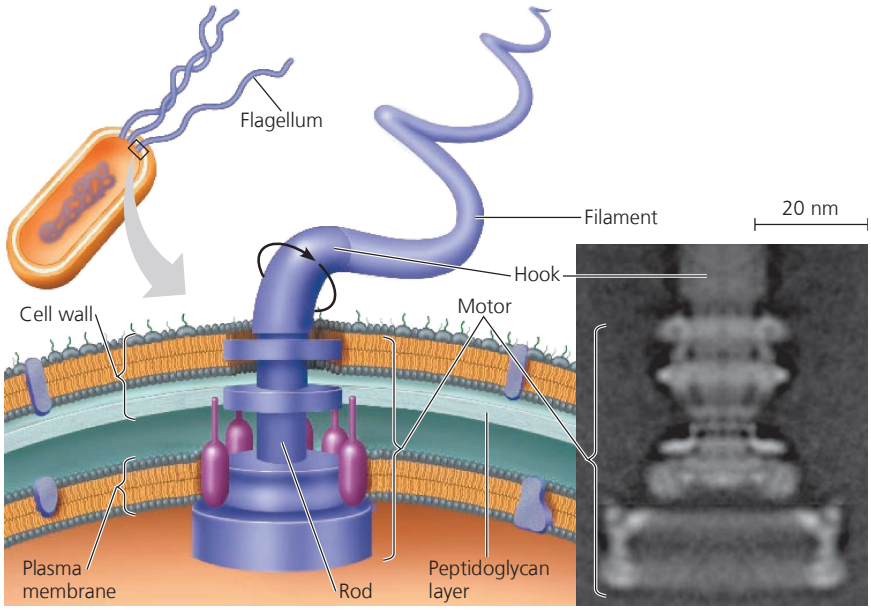
About half of all prokaryotes are capable of **taxis**, a directed movement toward or away from a stimulus (from the Greek *taxis*, to arrange). For example, prokaryotes that exhibit *chemotaxis* change their movement pattern in response to chemicals. They may move *toward* nutrients or oxygen (positive chemotaxis) or *away from* a toxic substance (negative chemotaxis). Some species can move at velocities exceeding 50 µm/sec—up to 50 times their body length per second. For perspective, consider that a person 1.7 m tall moving that fast would be running 306 km (190 miles) per hour!

Of the various structures that enable prokaryotes to move, the most common are flagella **(Figure 27.7)**. Flagella (singular, *flagellum*) may be scattered over the entire surface of the cell or concentrated at one or both ends. Prokaryotic flagella differ greatly from eukaryotic flagella: They are one-tenth the width and typically are not covered by an extension of the plasma membrane (see Figure 6.24). The flagella of prokaryotes and eukaryotes also differ in their molecular composition and their mechanism of propulsion. Among prokaryotes, bacterial and archaeal flagella are similar in size and rotational mechanism, but they are composed of entirely different and unrelated proteins. Overall, these structural and molecular comparisons indicate that the flagella of bacteria, archaea, and eukaryotes arose independently. Since current evidence shows that the flagella of organisms in the three domains perform similar functions but are not related by common descent, they are described as analogous, not homologous, structures (see Concept 22.3).

Evolutionary Origins of Bacterial Flagella

The bacterial flagellum shown in Figure 27.7 has three main parts (the motor, hook, and filament) that are themselves composed of 42 different kinds of proteins. How could such a complex structure evolve? In fact, much evidence indicates that bacterial flagella originated as simpler structures that were modified in a stepwise fashion over time. As in the case of the human eye (see Concept 25.6), biologists asked whether a less complex version of the flagellum could still benefit its owner. Analyses of hundreds of bacterial genomes indicate that only half of the flagellum's protein components appear to be necessary for it to function; the others are inessential or not encoded in the genomes of some species. Of the 21 proteins required by

▼ **Figure 27.7** **A prokaryotic flagellum.** The motor of a prokaryotic flagellum consists of a system of protein rings embedded in the cell wall and plasma membrane (TEM). The electron transport chain pumps protons out of the cell. The diffusion of protons back into the cell provides the force that turns a curved hook and thereby causes the attached filament to rotate and propel the cell. (This diagram shows flagellar structures characteristic of gram-negative bacteria.)



VISUAL SKILLS *Predict which of the four protein rings shown in this diagram are likely hydrophobic. Explain your answer.*

Mastering Biology **Video: Prokaryotic Flagella**

all species studied to date, 19 are modified versions of proteins that perform other tasks in bacteria. For example, a set of 10 proteins in the motor is homologous to 10 similar proteins in a secretory system found in bacteria. (A secretory system is a protein complex that enables a cell to produce and release certain macromolecules.) Two other proteins in the motor are homologous to proteins that function in ion transport. The proteins that comprise the rod, hook, and filament are all related to each other and are descended from an ancestral protein that formed a pilus-like tube. These findings suggest that the bacterial flagellum evolved as other proteins were added to an ancestral secretory system. This is an example of *exaptation*, the process in which structures originally adapted for one function take on new functions through descent with modification.

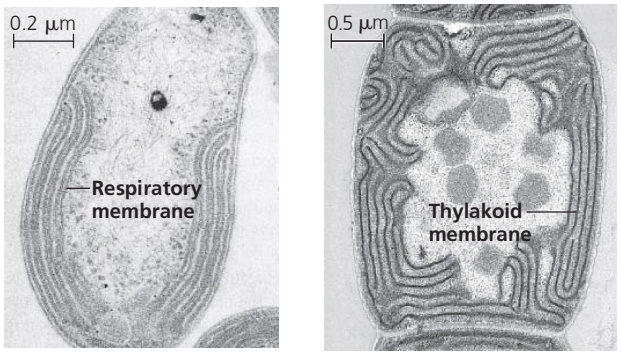
Internal Organization and DNA

The cells of prokaryotes are simpler than those of eukaryotes in both their internal structure and the physical arrangement of their DNA (see Figure 6.5). Prokaryotic cells lack the complex compartmentalization associated with the membrane-enclosed organelles found in eukaryotic cells. However, some prokaryotic cells do have specialized membranes that perform metabolic functions **(Figure 27.8)**. These membranes are usually infoldings of the plasma membrane. Recent discoveries also indicate that some prokaryotes can store metabolic by-products in simple compartments that are made out of proteins; these compartments do not have a membrane.

The genome of a prokaryote is structurally different from a eukaryotic genome and in most cases has considerably less DNA. Prokaryotes typically have one circular chromosome **(Figure 27.9)**, whereas eukaryotes usually have several to many linear chromosomes. In addition, in prokaryotes the chromosome is associated with many fewer proteins than are the chromosomes of eukaryotes. Also unlike eukaryotes, prokaryotes lack a nucleus; their chromosome is located in the **nucleoid**, a region of cytoplasm that is not enclosed by a membrane. In addition to its single chromosome, a typical prokaryotic cell may also have much smaller rings of independently replicating DNA molecules called **plasmids** (see Figure 27.9), most carrying only a few genes.

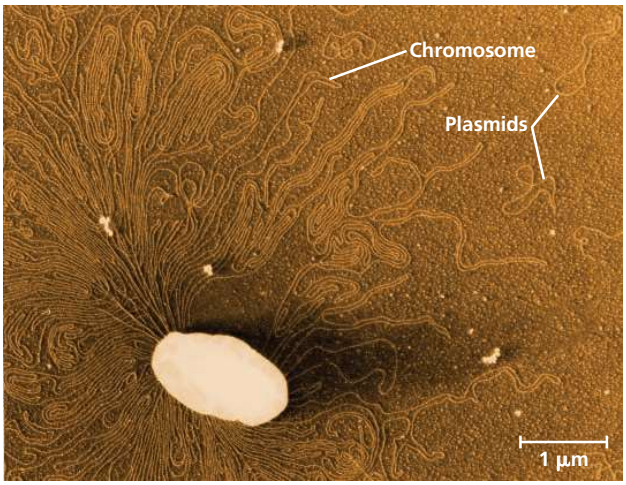
Although DNA replication, transcription, and translation are fundamentally similar processes in prokaryotes and eukaryotes, some of the details differ (see Chapter 17). For example, prokaryotic ribosomes are slightly smaller than eukaryotic ribosomes and differ in their protein and RNA content. These differences allow certain antibiotics, such as erythromycin and tetracycline, to bind to ribosomes and block protein synthesis in prokaryotes but not in eukaryotes. As a result, people can use these antibiotics to kill or inhibit the growth of bacteria without harming themselves.

▼ Figure 27.8 Specialized membranes of prokaryotes. **(a)** Infoldings of the plasma membrane, reminiscent of the cristae of mitochondria, function in cellular respiration in some aerobic prokaryotes (TEM). **(b)** Photosynthetic prokaryotes called cyanobacteria have thylakoid membranes, much like those in chloroplasts (TEM).



(a) Aerobic prokaryote **(b) Photosynthetic prokaryote**

▼ Figure 27.9 A prokaryotic chromosome and plasmids. The thin, tangled loops surrounding this ruptured *Escherichia coli* cell are parts of the cell's large, circular chromosome (colorized TEM). Three of the cell's plasmids, the much smaller rings of DNA, are also shown.



VISUAL SKILLS *Identify and label the third plasmid visible in this micrograph.*

Reproduction

Many prokaryotes can reproduce quickly in favorable environments. By *binary fission* (see Figure 12.12), a single prokaryotic cell divides into 2 cells, which then divide into 4, 8, 16, and so on. Under optimal conditions, many prokaryotes can divide every 1–3 hours; some species can produce a new generation in only 20 minutes. At this rate, a single prokaryotic cell could give rise to a colony outweighing Earth in only two days!

In reality, of course, this does not occur. The cells eventually exhaust their nutrient supply, poison themselves with metabolic wastes, face competition from other microorganisms, or are consumed by other organisms. Still, the potential of many prokaryotic species for rapid population

growth emphasizes three key features of their biology: *They are small, they reproduce by binary fission, and they often have short generation times*. As a result, prokaryotic populations can consist of many trillions of individuals—far more than populations of multicellular eukaryotes, such as plants or animals.

Mastering Biology **Animation: Structure and Reproduction of Bacteria**

CONCEPT CHECK 27.1

1. Describe two adaptations that enable prokaryotes to survive in environments too harsh for other organisms.
2. Contrast the cellular and DNA structures of prokaryotes and eukaryotes.
3. **MAKE CONNECTIONS** Suggest a hypothesis that explains why the thylakoid membranes of chloroplasts resemble those of cyanobacteria. Refer to Figures 6.18 and 26.21.

For suggested answers, see Appendix A.

CONCEPT 27.2

Rapid reproduction, mutation, and genetic recombination promote genetic diversity in prokaryotes

As we discussed in Unit Four, evolution cannot occur without genetic variation. The diverse adaptations exhibited by prokaryotes suggest that their populations must have considerable genetic variation—and they do. In this section, we'll examine three factors that give rise to high levels of genetic diversity in prokaryotes: rapid reproduction, mutation, and genetic recombination.

Rapid Reproduction and Mutation

Most of the genetic variation in sexually reproducing species results from the way existing alleles are arranged in new combinations during meiosis and fertilization (see Concept 13.4). Prokaryotes do not reproduce sexually, so at first glance their extensive genetic variation may seem puzzling. But in many species, this variation can result from a combination of rapid reproduction and mutation.

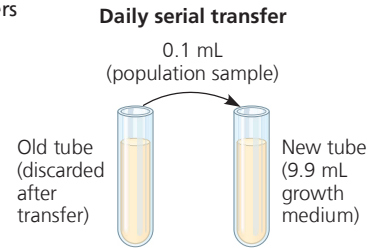
Consider the bacterium *Escherichia coli* as it reproduces by binary fission in a human intestine, one of its natural environments. After repeated rounds of division, most of the offspring cells are genetically identical to the original parent cell. However, if errors occur during DNA replication, some of the offspring cells may differ genetically. The probability of such a mutation occurring in a given *E. coli* gene is about one in 10 million (1×10^{-7}) per cell division. But among the 2×10^{10} new *E. coli* cells that arise each day in a person's intestine, there will be approximately $(2 \times 10^{10}) \times (1 \times 10^{-7}) = 2{,}000$ bacteria that have a mutation in that gene. The total number of new mutations when all 4,300 *E. coli* genes are considered is about $4{,}300 \times 2{,}000$—more than 8 million per day per human host.

The key point is that new mutations, though rare on a per gene basis, can increase genetic diversity quickly in species with short generation times and large populations. This diversity, in turn, can lead to rapid evolution **(Figure 27.10)**:

▼ Figure 27.10 Inquiry

Can prokaryotes evolve rapidly in response to environmental change?

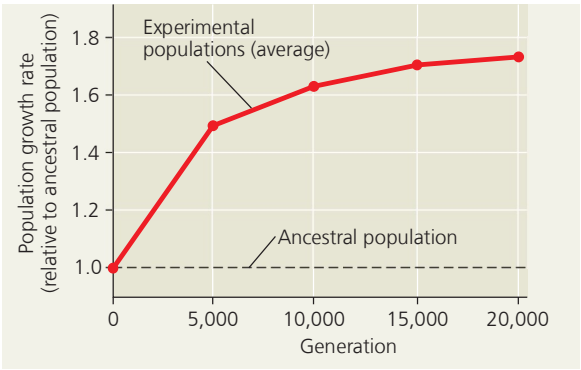
Experiment Researchers tested the ability of *E. coli* populations to adapt to a new environment. They established 12 populations, each founded by a single cell from an *E. coli* strain, and followed these populations for 20,000 generations (3,000 days).



To maintain a continual supply of resources, each day the researchers performed a *serial transfer*: They transferred 0.1 mL of each population to a new tube containing 9.9 mL of fresh growth medium. The growth medium used throughout the experiment provided a challenging environment that contained only low levels of glucose and other resources needed for growth.

Samples were periodically removed from the 12 populations and grown in competition with the common ancestral strain in the experimental (low-glucose) environment.

Results The fitness of the experimental populations, as measured by the growth rate of each population, increased rapidly for the first 5,000 generations (2 years) and more slowly for the next 15,000 generations. The graph shows the averages for the 12 populations.



Conclusion Populations of *E. coli* continued to accumulate beneficial mutations for 20,000 generations, allowing rapid evolution of increased population growth rates in their new environment.

Data from V. S. Cooper and R. E. Lenski, The population genetics of ecological specialization in evolving *Escherichia coli* populations, *Nature* 407:736–739 (2000).

WHAT IF? *Suggest possible functions of the genes whose sequence or expression was altered as the experimental populations evolved in the low-glucose environment.*

Individuals that are genetically better equipped for their environment tend to survive and reproduce at higher rates than other individuals. The ability of prokaryotes to adapt rapidly to new conditions highlights the point that although the structure of their cells is simpler than that of eukaryotic cells, prokaryotes are not "primitive" or "inferior" in an evolutionary sense. They are, in fact, highly evolved: For 3.5 billion years, prokaryotic populations have responded successfully to many types of environmental challenges.

Genetic Recombination

Although new mutations are a major source of variation in prokaryotic populations, additional diversity arises from *genetic recombination*, the combining of DNA from two sources. In eukaryotes, the sexual processes of meiosis and fertilization combine DNA from two individuals in a single zygote. But meiosis and fertilization do not occur in prokaryotes. Instead, three other mechanisms—transformation, transduction, and conjugation—can bring together prokaryotic DNA from different individuals (that is, different cells). When the individuals are members of different species, this movement of genes from one organism to another is called *horizontal gene transfer*. Scientists have found evidence that each of these mechanisms can transfer DNA within and between species in both domain Bacteria and domain Archaea. To date, however, most of our knowledge comes from research on bacteria.

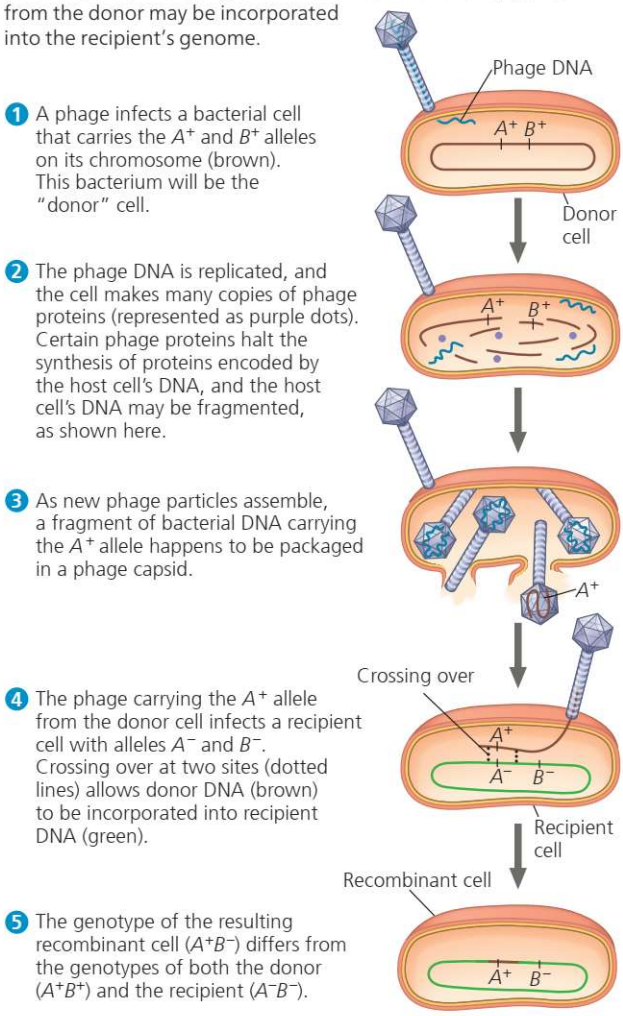
Transformation and Transduction

In **transformation**, the genotype and possibly phenotype of a prokaryotic cell are altered by the uptake of foreign DNA from its surroundings. For example, a harmless strain of *Streptococcus pneumoniae* can be transformed into pneumonia-causing cells if the cells are exposed to DNA from a pathogenic strain (see Figure 16.2). This transformation occurs when a nonpathogenic cell takes up a piece of DNA carrying the allele for pathogenicity and replaces its own allele with the foreign allele, an exchange of homologous DNA segments. The cell is now a recombinant: Its chromosome contains DNA derived from two different cells.

For many years after transformation was discovered in laboratory cultures, most biologists thought it was too rare and haphazard to play an important role in natural bacterial populations. But researchers have since learned that many bacteria have cell-surface proteins that recognize DNA from closely related species and transport it into the cell. Once inside the cell, the foreign DNA can be incorporated into the genome by homologous DNA exchange.

In **transduction**, phages (short for "bacteriophages," the viruses that infect bacteria) carry prokaryotic genes from one host cell to another. In most cases, transduction results from accidents that occur during the phage replicative cycle **(Figure 27.11)**. A virus that carries prokaryotic DNA may not be able to replicate because it lacks some or all of its own genetic material. However, the virus can attach to another prokaryotic cell (a recipient) and inject prokaryotic DNA acquired from the first cell (the donor). If some of this DNA is then incorporated into the recipient cell's chromosome by crossing over, a recombinant cell is formed.

▼ **Figure 27.11 Transduction.** Phages may carry pieces of a bacterial chromosome from one cell (the donor) to another (the recipient). If crossing over occurs after the transfer, genes from the donor may be incorporated into the recipient's genome.

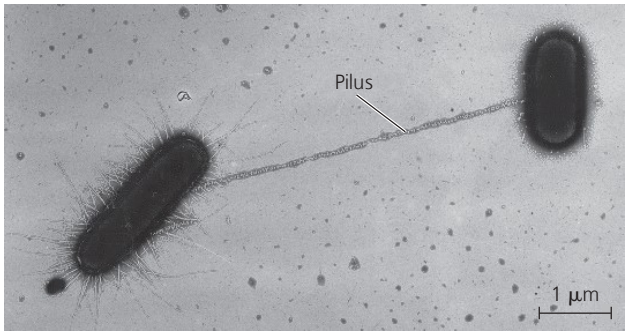


VISUAL SKILLS *Based on this diagram, describe the circumstances in which a transduction event would result in horizontal gene transfer.*

Conjugation and Plasmids

In a process called **conjugation**, DNA is transferred between two prokaryotic cells (usually of the same species) that are temporarily joined. In bacteria, the DNA transfer is always one-way: One cell donates the DNA, and the other receives it. We'll focus here on the mechanism used by *E. coli*.

▼ Figure 27.12 Bacterial conjugation. The *E. coli* donor cell (left) extends a pilus that attaches to a recipient cell, a key first step in the transfer of DNA. The pilus is a flexible tube of protein subunits (TEM).

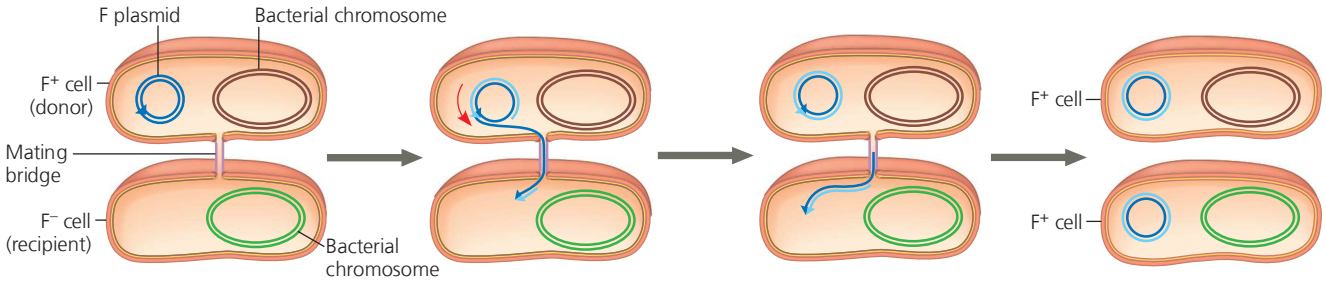


First, a pilus of the donor cell attaches to the recipient **(Figure 27.12)**. The pilus then retracts, pulling the two cells together, like a grappling hook. The next step is thought to be the formation of a temporary structure between the two cells, a "mating bridge" through which the donor may transfer DNA to the recipient. However, the mechanism by which DNA transfer occurs is unclear; indeed, recent evidence indicates that DNA may pass directly through the hollow pilus.

The ability to form pili and donate DNA during conjugation results from the presence of a particular piece of DNA called the **F factor** (F for fertility). The F factor of *E. coli* consists of about 25 genes, most required for the production of pili. As shown in **Figure 27.13**, the F factor can

▼ Figure 27.13 Conjugation and recombination in *E. coli*. The DNA replication that accompanies transfer of an F plasmid or part of an Hfr bacterial chromosome is called *rolling circle replication*. In effect, the intact circular parental DNA strand "rolls" as its other strand peels off and a new complementary strand is synthesized.

Mastering Biology
Figure Walkthrough



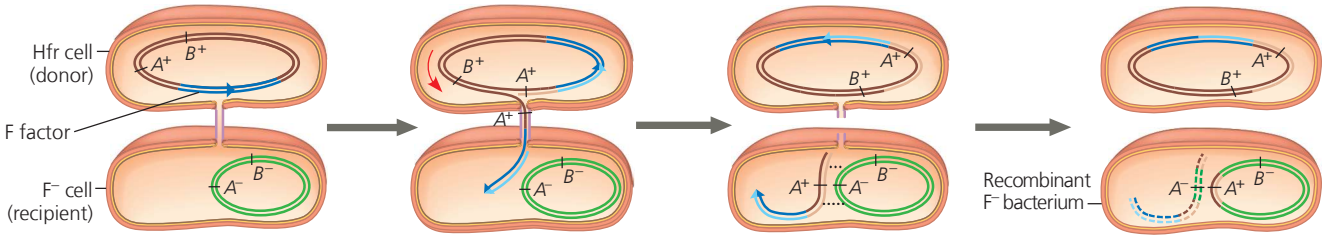
1 A cell carrying an F plasmid (an F^+ cell) forms a mating bridge with an F^- cell. One strand of the plasmid's DNA breaks at the point marked by the arrowhead.

2 Using the unbroken strand as a template, the cell synthesizes a new strand (light blue). Meanwhile, the broken strand peels off (red arrow), and one end enters the F^- cell. There, synthesis of its complementary strand begins.

3 DNA replication continues in both the donor and recipient cells, as the transferred plasmid strand moves farther into the recipient cell.

4 Once DNA transfer and synthesis are completed, the plasmid in the recipient cell circularizes. The recipient cell is now a recombinant F^+ cell.

(a) Conjugation and transfer of an F plasmid



1 In an Hfr cell, the F factor (dark blue) is integrated into the bacterial chromosome. Since an Hfr cell has all of the F factor genes, it can form a mating bridge with an F^- cell and transfer DNA.

2 A single strand of the F factor breaks and begins to move through the bridge. DNA replication occurs in both donor and recipient cells, resulting in double-stranded DNA (daughter strands shown in lighter color).

3 The mating bridge usually breaks before the entire chromosome is transferred. Crossing over at two sites (dotted lines) can result in the exchange of homologous genes (here, A^+ and A^-) between the transferred DNA (brown) and the recipient's chromosome (green).

4 Cellular enzymes degrade any linear DNA not incorporated into the chromosome. The recipient cell, with a new combination of genes but no F factor, is now a recombinant F^- cell.

(b) Conjugation and transfer of part of an Hfr bacterial chromosome, resulting in recombination. A^+/A^- and B^+/B^- indicate alleles for gene *A* and gene *B*, respectively.

exist either as a plasmid or as a segment of DNA within the bacterial chromosome.

The F Factor as a Plasmid The F factor in its plasmid form is called the **F plasmid**. Cells containing the F plasmid, designated F^+ cells, function as DNA donors during conjugation (see Figure 27.13a). Cells lacking the F factor, designated F^-, function as DNA recipients during conjugation. The F^+ condition is transferable in the sense that an F^+ cell converts an F^- cell to F^+ if a copy of the entire F plasmid is transferred. Even if this does not occur, as long as some of the F plasmid's DNA is transferred successfully to the recipient cell, that cell is now a recombinant cell.

The F Factor in the Chromosome Chromosomal genes can be transferred during conjugation when the donor cell's F factor is integrated into the chromosome. A cell with the F factor built into its chromosome is called an *Hfr cell* (for high frequency of recombination). Like an F^+ cell, an Hfr cell functions as a donor during conjugation with an F^- cell (see Figure 27.13b). When chromosomal DNA from an Hfr cell enters an F^- cell, homologous regions of the Hfr and F^- chromosomes may align, allowing segments of their DNA to be exchanged. As a result, the recipient cell becomes a recombinant bacterium that has genes derived from the chromosomes of two different cells—a new genetic variant on which evolution can act.

R Plasmids and Antibiotic Resistance Many species of bacteria have genes that code for enzymes that specifically destroy or otherwise hinder the effectiveness of certain antibiotics, such as tetracycline or ampicillin. Such "resistance genes" are often carried by plasmids known as **R plasmids** (R for resistance). Many R plasmids, like F plasmids, have genes that encode pili and enable DNA transfer from one bacterial cell to another by conjugation. As a result, R plasmids and the resistance genes they carry can spread rapidly through a bacterial population—a problem of great public health concern (see Concept 27.6). Making the problem still worse, some R plasmids carry genes for resistance to as many as ten antibiotics.

Mastering Biology BBC Video: A Future Without Antibiotics?

CONCEPT CHECK 27.2

1. Although rare on a per gene basis, new mutations can add considerable genetic variation to prokaryotic populations in each generation. Explain how this occurs.
2. Distinguish between the three mechanisms by which bacteria can transfer DNA from one bacterial cell to another.
3. **WHAT IF?** If a nonpathogenic bacterium were to acquire resistance to antibiotics, could this strain pose a health risk to people? In general, how does DNA transfer among bacteria affect the spread of resistance genes?

For suggested answers, see Appendix A.

CONCEPT 27.3

Diverse nutritional and metabolic adaptations have evolved in prokaryotes

The extensive genetic variation found in prokaryotes is reflected in their diverse nutritional adaptations. Like all organisms, prokaryotes can be categorized by how they obtain energy and the carbon used in building the organic molecules that make up cells. Every type of nutrition observed in eukaryotes is represented among prokaryotes, along with some nutritional modes unique to prokaryotes. In fact, prokaryotes have an astounding range of metabolic adaptations, much broader than that found in eukaryotes.

Organisms that obtain energy from light are called *phototrophs*, and those that obtain energy from chemicals are called *chemotrophs*. Organisms that need only CO_2 or related compounds as a carbon source are called *autotrophs*. In contrast, *heterotrophs* require at least one organic nutrient, such as glucose, to make other organic compounds. Combining the two energy sources with the two carbon sources results in four major modes of nutrition, summarized in **Table 27.1**.

Table 27.1 Major Nutritional Modes

Mode	Energy Source	Carbon Source	Types of Organisms
AUTOTROPH			
Photoautotroph	Light	CO_2, HCO_3^-, or related compound	Photosynthetic prokaryotes (for example, cyanobacteria); plants; certain protists (for example, algae)
Chemoautotroph	Inorganic chemicals (such as H_2S, NH_3, or Fe^{2+})	CO_2, HCO_3^-, or related compound	Unique to certain prokaryotes (for example, *Sulfolobus*)
HETEROTROPH			
Photoheterotroph	Light	Organic compounds	Unique to certain aquatic and salt-loving prokaryotes (for example, *Rhodobacter, Chloroflexus*)
Chemoheterotroph	Organic compounds	Organic compounds	Many prokaryotes (for example, *Clostridium*) and protists; fungi; animals; some plants

The Role of Oxygen in Metabolism

Prokaryotic metabolism also varies with respect to oxygen (O_2). **Obligate aerobes** must use O_2 for cellular respiration and cannot grow without it. **Obligate anaerobes**, on the other hand, are poisoned by O_2. Some obligate anaerobes live exclusively by fermentation; others extract chemical energy by **anaerobic respiration**, in which substances other than O_2, such as nitrate ions (NO_3^-) or sulfate ions (SO_4^{2-}), accept electrons at the "downhill" end of electron transport chains. **Facultative anaerobes** use O_2 if it is present but can also carry out fermentation or anaerobic respiration in an anaerobic environment.

Nitrogen Metabolism

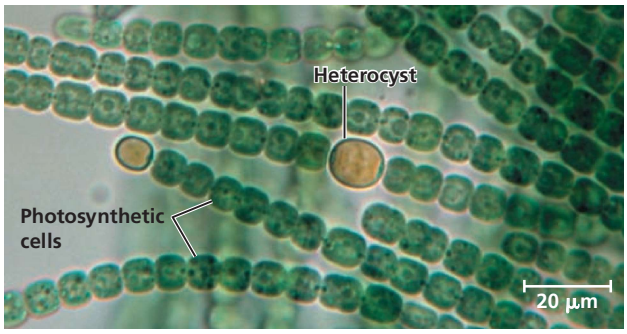
Nitrogen is essential for the production of amino acids and nucleic acids in all organisms. Whereas eukaryotes can obtain nitrogen only from a limited group of nitrogen compounds, prokaryotes can metabolize nitrogen in many forms. For example, some cyanobacteria and some methanogens (various archaea) convert atmospheric nitrogen (N_2) to ammonia (NH_3), a process called **nitrogen fixation**. The cells can then incorporate this "fixed" nitrogen into amino acids and other organic molecules. In terms of nutrition, nitrogen-fixing cyanobacteria are some of the most self-sufficient organisms since they need only light, CO_2, N_2, water, and some minerals to grow.

Nitrogen fixation has a large impact on other organisms. For example, nitrogen-fixing prokaryotes can increase the nitrogen available to plants, which cannot use atmospheric nitrogen but can use the nitrogen compounds that the prokaryotes produce from ammonia. Concept 55.4 discusses this and other essential roles that prokaryotes play in the nitrogen cycles of ecosystems.

Metabolic Cooperation

Cooperation between prokaryotic cells allows them to use environmental resources they could not use as individual cells. In some cases, this cooperation takes place between specialized cells of a filament. For instance, the cyanobacterium *Anabaena* has genes that encode proteins for photosynthesis and for nitrogen fixation. However, a single cell cannot carry out both processes at the same time because photosynthesis produces O_2, which inactivates the enzymes involved in nitrogen fixation. Instead of living as isolated cells, *Anabaena* forms filamentous chains **(Figure 27.14)**. Most cells in a filament carry out only photosynthesis, while a few specialized cells called **heterocysts** (sometimes called *heterocytes*) carry out only nitrogen fixation. Each heterocyst is surrounded by a thickened cell wall that restricts entry of O_2 produced by neighboring photosynthetic cells. Intercellular connections allow heterocysts to transport fixed nitrogen to neighboring cells and to receive carbohydrates.

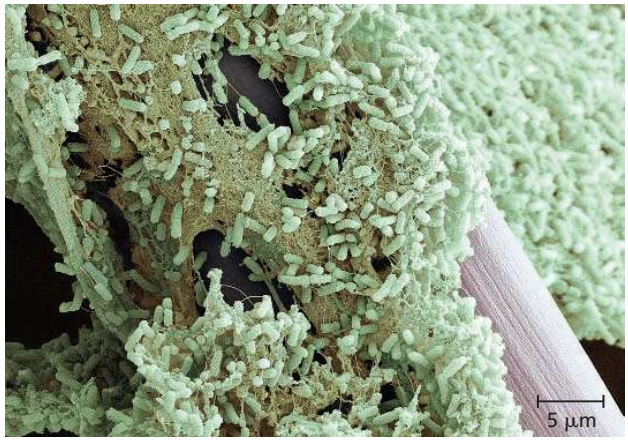
Metabolic cooperation among the cells of one or more prokaryotic species often occurs in surface-coating colonies known as **biofilms**. Cells in a biofilm secrete signaling molecules that recruit nearby cells, causing the colonies to grow. The cells also produce polysaccharides and proteins that stick the cells to the substrate and to one another; these polysaccharides and proteins form the capsule, or slime layer, mentioned earlier in the chapter. Channels in the biofilm allow nutrients to reach cells in the interior and wastes to be expelled.



▲ **Figure 27.14 Metabolic cooperation in a prokaryote.** In the filamentous freshwater cyanobacterium *Anabaena*, heterocysts fix nitrogen, while the other cells carry out photosynthesis (LM).

Biofilms are common in nature, but they can cause a wide range of problems for humans. For example, biofilms growing in pipes slow the flow of liquids such as water or oil and degrade the pipes themselves. Biofilms also corrode boat hulls, oil platforms, and many other structures and industrial products. In medical settings, biofilms can contaminate contact lenses, catheters, pacemakers, heart valves, artificial joints, and many other devices. They also contribute to tooth decay and a wide range of chronic infections **(Figure 27.15)**, some of which can be lethal. Many biofilms can evade host immune responses and are extremely resistant to antibiotics, making them hard to treat. Altogether, each year biofilms cause billions of dollars in damage and inflict tens of millions of people with chronic infections.

▼ **Figure 27.15 *Pseudomonas aeruginosa* forming a biofilm (colorized SEM).** This widespread bacterial species can be found in soil and water and as part of the normal community in the human intestines. *P. aeruginosa* can cause serious infections of other human organs, including the skin, urinary tract, and lungs. These infections can be difficult to treat, in part because the bacteria can grow as biofilms that have increased resistance to antibiotics.



CONCEPT CHECK 27.3

1. Distinguish between the four major modes of nutrition, noting which are unique to prokaryotes.
2. A bacterium requires only the amino acid methionine as an organic nutrient and lives in lightless caves. What mode of nutrition does it employ? Explain.
3. **WHAT IF?** Describe what you might eat for a typical meal if humans, like cyanobacteria, could fix nitrogen.

For suggested answers, see Appendix A.

CONCEPT 27.4

Prokaryotes have radiated into a diverse set of lineages

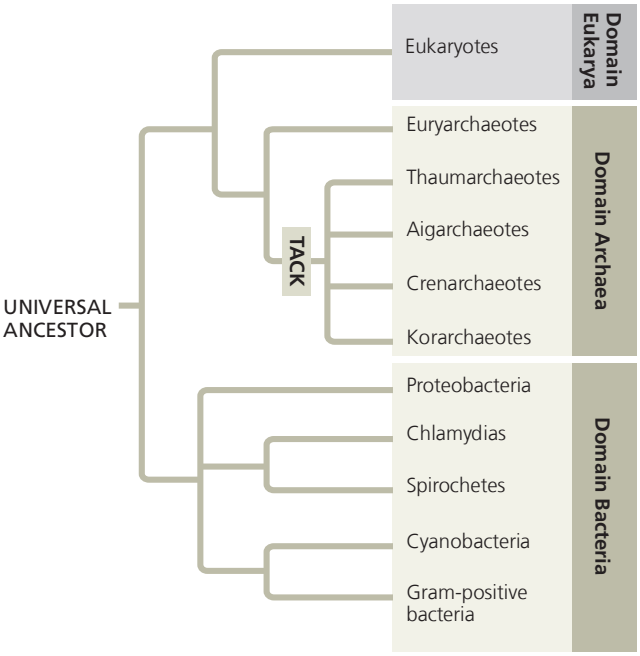
Since their origin 3.5 billion years ago, prokaryotic populations have radiated extensively as a wide range of structural and metabolic adaptations have evolved in them. Collectively, these adaptations have enabled prokaryotes to inhabit every environment known to support life—if there are organisms in a particular place, some of those organisms are prokaryotes. Yet despite their obvious success, it is only in recent decades that advances in genomics have begun to reveal the full extent of prokaryotic diversity.

An Overview of Prokaryotic Diversity

In the 1970s, microbiologists began using small-subunit ribosomal RNA as a marker for evolutionary relationships. Their results indicated that many prokaryotes once classified as bacteria are actually more closely related to eukaryotes and belong in a domain of their own: Archaea. Microbiologists have since analyzed larger amounts of genetic data—including more than 1,700 entire genomes—and have concluded that a few traditional groups, such as cyanobacteria, are monophyletic. However, other traditional groups, such as gram-negative bacteria, are scattered throughout several lineages. **Figure 27.16** shows one phylogenetic hypothesis for some of the major taxa of prokaryotes based on molecular systematics.

One lesson from studying prokaryotic phylogeny is that the genetic diversity of prokaryotes is immense. When researchers began to sequence the genes of prokaryotes, they could investigate only the small fraction of species that could be cultured in the laboratory. In the 1980s, researchers began using the polymerase chain reaction (PCR; see Figure 20.8) to analyze the genes of prokaryotes collected from the environment (such as from soil or water samples). Such "genetic prospecting" is now widely used; in fact, today entire prokaryotic genomes can be obtained from environmental samples using *metagenomics* (see Concept 21.1). Each year these techniques add new branches to the tree of life. While only about 16,000 prokaryotic species worldwide have been assigned scientific names, a single handful of soil could contain 10,000 prokaryotic species by some estimates. Taking full stock of this diversity will require many years of research.

▼ Figure 27.16 A simplified phylogeny of prokaryotes. This tree shows relationships among major prokaryotic groups; some of these relationships are shown as polytomies to reflect their uncertain order of divergence. Recent studies indicate that within Archaea, the thaumarchaeotes, aigarchaeotes, crenarchaeotes, and korarchaeotes are closely related; systematists have placed them in a supergroup called "TACK" in reference to the first letters of their names.



VISUAL SKILLS *Based on this phylogenetic tree diagram, which domain is the sister group of Archaea?*

Another important lesson from molecular systematics is that horizontal gene transfer has played a key role in the evolution of prokaryotes. Over hundreds of millions of years, prokaryotes have acquired genes from even distantly related species, and they continue to do so today. As a result, significant portions of the genomes of many prokaryotes are actually mosaics of genes imported from other species. For example, a study of 329 sequenced bacterial genomes found that an average of 75% of the genes in each genome had been transferred horizontally at some point in their evolutionary history. As we saw in Concept 26.6, such gene transfers can make it difficult to determine phylogenetic relationships. Still, it is clear that for billions of years, the prokaryotes have evolved in two separate lineages, the bacteria and the archaea (see Figure 27.16).

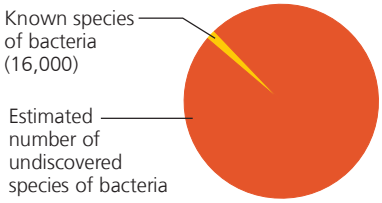
Bacteria



As surveyed in **Figure 27.17**, bacteria include the vast majority of prokaryotic species familiar to most people, from the pathogenic species that cause strep throat and tuberculosis to the beneficial species used to make Swiss cheese and yogurt.

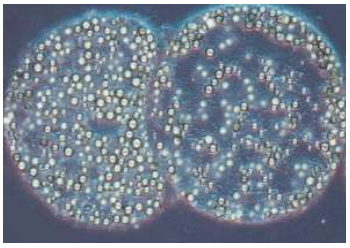
▼ Figure 27.17 Exploring Bacterial Diversity

This figure highlights a few key groups of bacteria, but their actual diversity is far greater than shown here. Likewise, gene sequence data indicate that the 16,000 known species of bacteria represent a small fraction of the actual number, estimated at 700,000–1.4 million species.



Proteobacteria

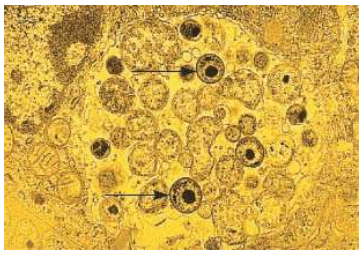
This large and diverse clade of gram-negative bacteria includes photoautotrophs, chemoautotrophs, and heterotrophs. One autotroph, the sulfur bacterium *Thiomargarita namibiensis*, obtains energy by oxidizing H_2S, producing sulfur as a waste product (the small globules in the photograph below). Heterotrophs include pathogens such as *Neisseria gonorrhoeae*, which causes gonorrhea; *Vibrio cholerae*, which causes cholera; and *Helicobacter pylori*, which causes stomach ulcers. Current evidence indicates that mitochondria evolved by endosymbiosis from a heterotroph in the subgroup alpha proteobacteria.



Thiomargarita namibiensis containing sulfur wastes (LM)

Chlamydias

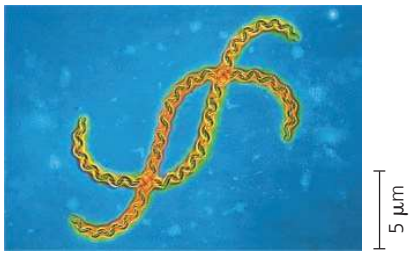
These parasites can survive only within animal cells, depending on their hosts for resources as basic as ATP. The gram-negative walls of chlamydias are unusual in that they lack peptidoglycan. One species, *Chlamydia trachomatis*, is the most common cause of blindness in the world and also causes nongonococcal urethritis, the most common sexually transmitted disease in the United States.



Chlamydia (arrows inside an animal cell (colorized TEM)

Spirochetes

These helical gram-negative heterotrophs spiral through their environment by means of rotating, internal, flagellum-like filaments. Many spirochetes are free-living, but others are notorious pathogenic parasites: *Treponema pallidum* causes syphilis, and *Borrelia burgdorferi* causes Lyme disease.



Leptospira, a spirochete (colorized TEM)

Cyanobacteria

These gram-negative photoautotrophs are the only prokaryotes with plantlike, oxygen-generating photosynthesis. (In fact, chloroplasts are thought to have evolved from an endosymbiotic cyanobacterium.) Both solitary and filamentous cyanobacteria are abundant components of freshwater and marine *phytoplankton*, the collection of small photosynthetic organisms that drift near the water's surface.



Cylindrospermum, a filamentous cyanobacterium

Gram-Positive Bacteria

Gram-positive bacteria rival the proteobacteria in diversity. Species in one subgroup, the actinomycetes, form colonies containing branched chains of cells; two of these species cause tuberculosis and leprosy, but most are decomposers living in soil. Soil-dwelling species in the genus *Streptomyces* are cultured as a source of antibiotics, including tetracycline and erythromycin. Other subgroups of gram-positive bacteria include pathogens such as *Staphylococcus aureus* (see Figure 22.14), *Bacillus anthracis*, which causes anthrax, and *Clostridium botulinum*, which causes botulism.



Streptomyces, the source of many antibiotics (SEM)

Every major mode of nutrition and metabolism is represented among the 80 or so phyla of bacteria, and even a small group of bacteria may contain species exhibiting many different nutritional modes. As we'll see, the diverse nutritional and metabolic capabilities of bacteria—and archaea—are behind the great impact these organisms have on Earth and its life.

Archaea



Archaea share certain traits with bacteria and other traits with eukaryotes **(Table 27.2)**. However, archaea also have many unique characteristics, as we would expect in a taxon that has followed a separate evolutionary path for so long.

The first prokaryotes assigned to domain Archaea live in environments so extreme that few other organisms can survive there. Such organisms are called **extremophiles**, meaning "lovers" of extreme conditions (from the Greek *philos*, lover), and include extreme halophiles and extreme thermophiles.

Extreme halophiles (from the Greek *halo*, salt) live in highly saline environments, such as the Great Salt Lake in Utah, the Dead Sea in Israel, and the Spanish lake shown in Figure 27.1. Some species merely tolerate salinity, while others require an environment that is several times saltier than seawater (which has a salinity of 3.5%). For example, the proteins and cell wall of *Halobacterium* have unusual features that improve function in extremely salty environments but render these organisms incapable of survival if the salinity drops below 9%.

Table 27.2 A Comparison of the Three Domains of Life

CHARACTERISTIC	DOMAIN		
	Bacteria	Archaea	Eukarya
Nuclear envelope	Absent	Absent	Present
Membrane-enclosed organelles	Absent	Absent	Present
Peptidoglycan in cell wall	Present	Absent	Absent
Membrane lipids	Unbranched hydrocarbons	Some branched hydrocarbons	Unbranched hydrocarbons
RNA polymerase	One kind	Several kinds	Several kinds
Initiator amino acid for protein synthesis	Formyl-methionine	Methionine	Methionine
Introns in genes	Very rare	Present in some genes	Present in many genes
Response to the antibiotics streptomycin and chloramphenicol	Growth usually inhibited	Growth not inhibited	Growth not inhibited
Histones associated with DNA	Absent	Present in some species	Present
Circular chromosome	Present	Present	Absent
Growth at temperatures > 100°C	No	Some species	No



▲ Figure 27.18 Extreme thermophiles. Orange and yellow colonies of thermophilic prokaryotes grow in the hot water of Yellowstone National Park's Grand Prismatic Spring.

MAKE CONNECTIONS *How might the enzymes of thermophiles differ from those of other organisms? (Review enzymes in Concept 8.4.)*

Extreme thermophiles (from the Greek *thermos*, hot) thrive in very hot environments. For example, the archaean *Pyrococcus furiosus* lives in geothermally heated marine sediments that reach temperatures of 100°C. At temperatures this high, the cells of most organisms die because their DNA does not remain in a double helix and many of their proteins denature. *P. furiosus* and other extreme thermophiles avoid this fate because they have structural and biochemical adaptations that make their DNA and proteins stable at high temperatures—a feature that has enabled *P. furiosus* to be used in biotechnology as a source of DNA polymerase for the PCR technique (see Figure 20.8). Other examples of extreme thermophiles include archaea in the genus *Sulfolobus*, which live in sulfur-rich volcanic springs **(Figure 27.18)**. One extreme thermophile that lives near deep-sea hot springs called *hydrothermal vents* is informally known as "strain 121" since it can reproduce even at 121°C.

Many other archaea live in more moderate environments. Consider **methanogens**, archaea that release methane as a by-product of how they obtain energy. Many methanogens use CO_2 to oxidize H_2, a process that produces both energy and methane waste. Among the strictest of anaerobes, methanogens are poisoned by O_2. Although some methanogens live in extreme environments, such as under kilometers of ice in Greenland, others live in swamps and marshes where other microorganisms have consumed all the O_2. The "marsh gas" found in such environments is the methane released by these archaea. Other species inhabit the anaerobic guts of cattle, termites, and other herbivores, playing an essential role in the nutrition of these animals. Methanogens

are also useful to humans as decomposers in sewage treatment facilities.

Many extreme halophiles and most known methanogens are archaea in the clade Euryarchaeota (from the Greek *eurys*, broad, a reference to their wide habitat range). The euryarchaeotes also include some extreme thermophiles, though most thermophilic species belong to a second clade, Crenarchaeota (*cren* means "spring," such as a hydrothermal spring). Metagenomic studies have identified many species of euryarchaeotes and crenarchaeotes that are not extremophiles. These archaea exist in habitats ranging from farm soils to lake sediments to the surface of the open ocean.

New findings continue to inform our understanding of archaeal phylogeny. For example, recent metagenomic studies have uncovered the genomes of many species that are not members of Euryarchaeota or Crenarchaeota. Moreover, phylogenomic analyses show that three of these newly discovered groups—the Thaumarchaeota, Aigarchaeota, and Korarchaeota—are more closely related to the Crenarchaeota than they are to the Euryarchaeota. These findings have led to the identification of a "supergroup" that contains the Thaumarchaeota, Aigarchaeota, Crenarchaeota, and Korarchaeota (see Figure 27.16). This supergroup is referred to as "TACK" based on the names of the groups it includes.

The importance of the TACK supergroup was highlighted by the recent discovery of the lokiarchaeotes, a group that is closely related to TACK archaea and that may represent the long-sought-after sister group of the eukaryotes. As such, the characteristics of lokiarchaeotes may shed light on one of the major puzzles of biology today—how eukaryotes arose from their prokaryotic ancestors. The pace of these and other recent discoveries suggests that as metagenomic prospecting continues, the tree in Figure 27.16 will likely undergo further changes.

CONCEPT CHECK 27.4

1. Explain how molecular systematics and metagenomics have contributed to our understanding of the phylogeny and evolution of prokaryotes.
2. **DRAW IT** Redraw Figure 27.16 assuming that eukaryotes are more closely related to TACK archaea than to euryarchaeotes. Under this assumption, would the three domains shown in Figure 27.16 be valid? Explain.

For suggested answers, see Appendix A.

CONCEPT 27.5

Prokaryotes play crucial roles in the biosphere

If people were to disappear from the planet tomorrow, life on Earth would change for many species, but few would be driven to extinction. In contrast, prokaryotes are so important to the biosphere that if they were to disappear, the prospects of survival for many other species would be dim.

Chemical Recycling

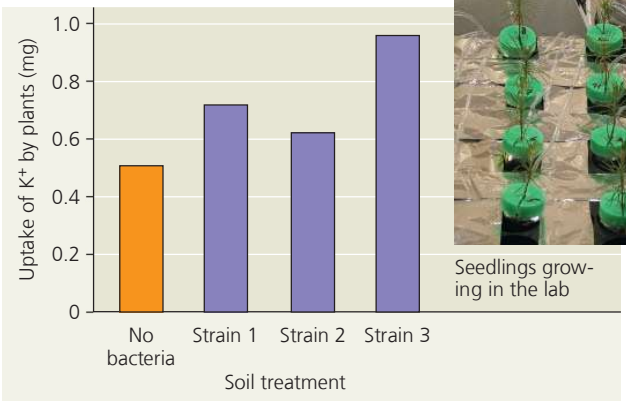
The atoms that make up the organic molecules in all living things were at one time part of inorganic substances in the soil, air, and water. Sooner or later, those atoms will return to the nonliving environment. Ecosystems depend on the continual recycling of chemical elements between the living and nonliving components of the environment, and prokaryotes play a major role in this process. For example, some chemoheterotrophic prokaryotes function as **decomposers**, breaking down dead organisms as well as waste products and thereby unlocking supplies of carbon, nitrogen, and other elements. Without the actions of prokaryotes and other decomposers such as fungi, life as we know it would cease. (See Concept 55.4 for a detailed discussion of chemical cycles.)

Prokaryotes also convert some molecules to forms that can be taken up by other organisms. Cyanobacteria and other autotrophic prokaryotes use CO_2 to make organic compounds such as sugars, which are then passed up through food chains. Cyanobacteria also produce atmospheric O_2, and a variety of prokaryotes fix atmospheric nitrogen (N_2) into forms that other organisms can use to make the building blocks of proteins and nucleic acids. Under some conditions, prokaryotes can increase the availability of nutrients that plants require for growth, such as nitrogen, phosphorus, and potassium **(Figure 27.19)**. Prokaryotes can also *decrease* the availability of key plant nutrients; this occurs when prokaryotes "immobilize" nutrients by using them to synthesize molecules

▼ Figure 27.19 Impact of bacteria on soil nutrient availability. Pine seedlings grown in sterile soils to which one of three strains of the bacterium *Burkholderia glathei* had been added absorbed more potassium (K^+) than did seedlings grown in soil without any bacteria. Other results (not shown) demonstrated that strain 3 increased the amount of K^+ released from mineral crystals to the soil.



Seedlings growing in the lab



WHAT IF? *Estimate the average uptake of K^+ for seedlings in soils with bacteria. What would you expect this average to be if bacteria had no effect on nutrient availability?*

that remain within their cells. Thus, prokaryotes can have complex effects on soil nutrient concentrations. In marine environments, an archaean from the clade Crenarchaeota can perform nitrification, a key step in the nitrogen cycle (see Figure 55.14). Crenarchaeotes dominate the oceans by numbers, comprising an estimated 10^{28} cells. The sheer abundance of these organisms suggests that they may have a large impact on the global nitrogen cycle.

Ecological Interactions

Prokaryotes play a central role in many ecological interactions. Consider **symbiosis** (from a Greek word meaning "living together"), an ecological relationship in which two species live in close contact with each other. Prokaryotes often form symbiotic associations with much larger organisms. In general, the larger organism in a symbiotic relationship is known as the **host**, and the smaller is known as the **symbiont**. There are many cases in which a prokaryote and its host participate in **mutualism**, an ecological interaction between two species in which both benefit **(Figure 27.20)**. Other interactions take the form of **commensalism**, an ecological relationship in which one species benefits while the other is not harmed or helped in any significant way. For example, more than 150 bacterial species live on the outer surface of your body, covering portions of your skin with up to 10 million cells per square centimeter. Some of these species are commensalists: You provide them with food, such as the oils that exude from your pores, and a place to live, while they neither harm nor benefit you. Finally, some symbiotic prokaryotes engage in **parasitism**, an ecological relationship in which a **parasite** feeds on the cell contents, tissues, or body fluids of its host. As a group, parasites harm but usually do not kill their host, at least not immediately (unlike a predator). Parasites that cause disease are known as **pathogens**, many of which are prokaryotic. (We'll discuss mutualism, commensalism, and parasitism in greater detail in Concept 54.1.)

The very existence of an ecosystem can depend on prokaryotes. For example, consider the diverse ecological communities found at hydrothermal vents. These communities are densely populated by many different kinds of animals, including worms, clams, crabs, and fishes. But since sunlight does not penetrate to the deep ocean floor, the community does not include photosynthetic organisms. Instead, the energy that supports the community is derived from the metabolic activities of chemoautotrophic bacteria. These bacteria harvest chemical energy from compounds such as hydrogen sulfide (H_2S) that are released from the vent. An active hydrothermal vent may support hundreds of eukaryotic species, but when the vent stops releasing chemicals, the chemoautotrophic bacteria cannot survive. As a result, the entire vent community collapses.

▼ Figure 27.20 Mutualism: bacterial "headlights." The glowing oval below the eye of the flashlight fish (*Photoblepharon palpebratus*) is an organ harboring bioluminescent bacteria. The fish uses the light to attract prey and to signal potential mates. The bacteria receive nutrients from the fish.



Mastering Biology Interview with Penny Chisholm: Studying the role of cyanobacteria in marine ecosystems (see the interview before Chapter 26)



CONCEPT CHECK 27.5

1. Explain how prokaryotes, though small, can be considered giants in their collective impact on Earth and its life.
2. **MAKE CONNECTIONS** Review Figure 10.5. Then summarize the main steps by which cyanobacteria produce O_2 and use CO_2 to make organic compounds.

For suggested answers, see Appendix A.

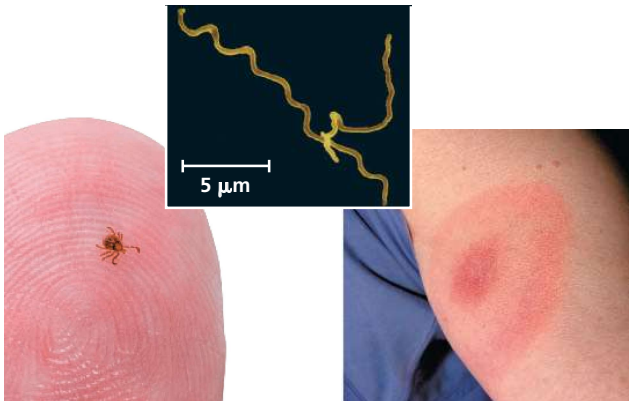
CONCEPT 27.6

Prokaryotes have both beneficial and harmful impacts on humans

Although the best-known prokaryotes tend to be the bacteria that cause human illness, these pathogens represent only a small fraction of prokaryotic species. Many other prokaryotes have positive interactions with people, and some play essential roles in agriculture and industry.

Mutualistic Bacteria

As is true for many other eukaryotes, human well-being can depend on mutualistic prokaryotes. For example, our intestines are home to an estimated 500–1,000 species of bacteria; collectively, their cells outnumber all human cells in the body by a factor of ten. Different species live in different portions of the intestines, and they vary in their ability to process different foods. Many of these species are mutualists, digesting food that our own intestines cannot break down. The genome of one of these gut mutualists, *Bacteroides thetaiotaomicron*, includes a large array of genes involved in synthesizing carbohydrates, vitamins, and other nutrients needed by



▲ **Figure 27.21 Lyme disease.** Ticks in the genus *Ixodes* spread the disease by transmitting the spirochete *Borrelia burgdorferi* (colorized SEM). A rash may develop at the site of the tick's bite; the rash may be large and ring-shaped (as shown) or much less distinctive.

humans. Signals from the bacterium activate human genes that build the network of intestinal blood vessels necessary to absorb nutrient molecules. Other signals induce human cells to produce antimicrobial compounds to which *B. thetaiotaomicron* is not susceptible. This action may reduce the population sizes of other, competing species, thus potentially benefiting both *B. thetaiotaomicron* and its human host.

Pathogenic Bacteria

All the pathogenic prokaryotes known to date are bacteria, and they deserve their negative reputation. Bacteria cause about half of all human diseases. For example, more than 1.5 million people die each year of the lung disease tuberculosis, caused by *Mycobacterium tuberculosis*. And another 2 million people die each year from diarrheal diseases caused by various bacteria.

Some bacterial diseases are transmitted by other species, such as fleas or ticks. In the United States, the most widespread pest-carried disease is Lyme disease, which infects about 300,000 people each year according to a recent CDC estimate **(Figure 27.21)**. Caused by a bacterium carried by ticks, Lyme disease can result in debilitating arthritis, heart disease, nervous disorders, and death if untreated.

Pathogenic prokaryotes usually cause illness by producing poisons, which are classified as exotoxins or endotoxins. **Exotoxins** are proteins secreted by certain bacteria and other organisms. Cholera, a dangerous diarrheal disease, is caused by an exotoxin secreted by the proteobacterium *Vibrio cholerae*. The exotoxin stimulates intestinal cells to release chloride ions into the gut, and water follows by osmosis. In another example, the potentially fatal disease botulism is caused by botulinum toxin, an exotoxin secreted by the gram-positive bacterium *Clostridium botulinum* as it ferments various foods, including improperly canned meat, seafood, and vegetables. Like other exotoxins, the botulinum toxin can produce disease even if the bacteria that manufacture it are no longer present when the food is eaten.

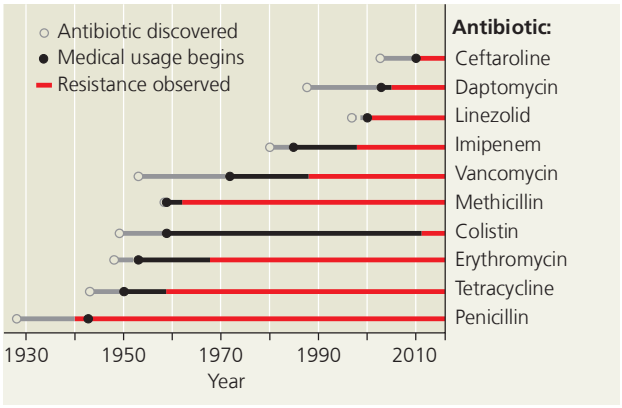
Endotoxins are lipopolysaccharide components of the outer membrane of gram-negative bacteria. In contrast to exotoxins, endotoxins are released only when the bacteria die and their cell walls break down. Endotoxin-producing bacteria include species in the genus *Salmonella*, such as *Salmonella typhi*, which causes typhoid fever. You might have heard of food poisoning caused by other *Salmonella* species that can be found in poultry and some fruits and vegetables.

Finally, horizontal gene transfer can spread genes associated with virulence, turning normally harmless bacteria into potent pathogens. *E. coli*, for instance, is ordinarily a harmless symbiont in the human intestines, but pathogenic strains that cause bloody diarrhea have emerged. One of the most dangerous strains, O157:H7, is a global threat; in the United States alone, there are around 75,000 cases of O157:H7 infection per year, often from contaminated beef or produce. Scientists have discovered over 1,000 genes in O157:H7 that have no counterpart in harmless *E. coli* strains. Some of the genes found only in O157:H7 are associated with virulence and were likely transferred by phage-mediated horizontal gene transfer (transduction) from pathogenic bacterial species.

Antibiotic Resistance

Since their initial use in the 1940s, antibiotics have saved many lives and reduced the incidence of disease caused by pathogenic bacteria. Unfortunately, as **Figure 27.22** shows,

▼ **Figure 27.22 The rise of antibiotic resistance.** As illustrated by the examples shown here, bacteria have developed resistance to every antibiotic currently in clinical use, often within a few years. It took more than 50 years for resistance to develop to colistin, most likely because this antibiotic has toxic side effects in humans and hence was used rarely (as a treatment of last resort).



VISUAL SKILLS *Based on this diagram, identify the antibiotic for which resistance appeared before the antibiotic began to be used medicinally.*

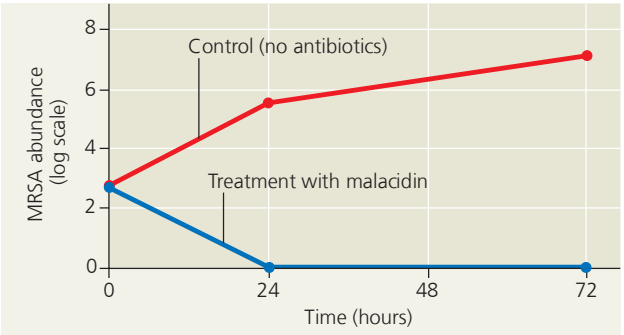
resistance to antibiotics has evolved in many bacteria, often rapidly. Compounding this problem, the discovery of new antibiotics has not kept pace with the rate at which resistance has evolved in bacteria. We now face a major public health concern: For every antibiotic now in use, at least one species of bacteria has developed resistance to it.

The rise of antibiotic resistance is driven by several factors. The rapid reproduction of bacteria enables cells carrying resistance genes to quickly produce large numbers of resistant offspring. Thus, when humans use antibiotics in medical or agricultural settings, natural selection can cause the fraction of a bacterial population carrying genes for antibiotic resistance to increase rapidly. Resistance genes also can spread within and among bacterial species by horizontal gene transfer. As a result, bacterial strains that are resistant to multiple antibiotics are becoming more common, making the treatment of certain bacterial infections very difficult.

Consider tuberculosis, the leading cause of death by infectious disease worldwide. The recent rise of drug-resistant strains of the tuberculosis bacterium (*Mycobacterium tuberculosis*) threatens decades of progress in combating tuberculosis. "Superbug" tuberculosis strains came to public notice in 2006, when an outbreak in a rural area of South Africa killed 52 of the 53 patients infected with what is now called extensively drug-resistant tuberculosis (XDR-TB). As of 2017, more than 100 countries had confirmed cases of XDR-TB. There are few treatments for XDR-TB, and those we have are difficult to administer and more toxic than are treatments for standard strains of the tuberculosis bacterium.

M. tuberculosis is not the only bacterium in which resistance to multiple antibiotics has evolved. Highly resistant strains have also been found in species that cause potentially lethal infections of the skin, lungs, digestive tract, and other human organs. Even so, recent discoveries give cause for hope. In 2018, for example, researchers used a metagenomic approach to sequence genes from soil bacteria that could not be grown in the laboratory. They found that some of these genes encoded a new class of antibiotics, which have been named *malacidins*. Malacidins have been effective against multidrug-resistant gram-positive pathogens, including clone USA300 **(Figure 27.23)**, a highly virulent strain of methicillin-resistant *Staphylococcus aureus* (MRSA; see Figure 22.14). Also in 2018, other researchers developed virus-like particles capable of targeting (and killing) particular species of multidrug-resistant bacteria. In recent years, novel approaches for growing soil bacteria in the laboratory also have led to the discovery of new antibiotics, as you can explore in the **Scientific Skills Exercise**.

▼ Figure 27.23 Effectiveness of malacidin against MRSA clone USA300. Treatment with malacidin rapidly cleared a skin infection in rats caused by clone USA300, a highly virulent strain of methicillin-resistant *Staphylococcus aureus* (MRSA). Malacidin was as effective as daptomycin, an antibiotic used to treat life-threatening infections.



Prokaryotes in Research and Technology

On a positive note, we reap many benefits from the metabolic capabilities of both bacteria and archaea. For example, people have long used bacteria to convert milk to cheese and yogurt. Bacteria are also used in the production of beer and wine, pepperoni, fermented cabbage (sauerkraut), and soy sauce. In recent decades, our greater understanding of prokaryotes has led to an explosion of new applications in biotechnology. Examples include the use of *E. coli* in gene cloning (see Figure 20.4) and the use of DNA polymerase from *Pyrococcus furiosus* in the PCR technique (see Figure 20.8). Through genetic engineering, we can modify bacteria to produce vitamins, antibiotics, hormones, and other products (see Concept 20.1).

Recently, the prokaryotic CRISPR-Cas system, which helps bacteria and archaea defend against attack by viruses (see Figure 19.7), has been developed into a powerful new tool for altering genes in virtually any organism. The genomes of many prokaryotes contain short DNA repeats, called CRISPRs, that interact with proteins known as the Cas (CRISPR-associated) proteins. Cas proteins, acting together with "guide RNA" made from the CRISPR region, can cut any DNA sequence to which they are directed. Scientists have been able to exploit this system by introducing a Cas protein (Cas9) to guide RNA into cells whose DNA they want to alter (see Figure 17.28). Among other applications, this **CRISPR-Cas9 system** has already opened new lines of research on HIV, the virus that causes AIDS **(Figure 27.24)**. While the CRISPR-Cas9 system can potentially be used in many different ways, care must be taken to guard against the unintended consequences that could arise when applying such a new and powerful technology.

Another valuable application of bacteria is to reduce our use of petroleum. Consider the plastics industry. Globally,

Scientific Skills Exercise

Calculating and Interpreting Means and Standard Errors



▶ **Plastic chip used to grow soil bacteria**

Can Antibiotics Obtained from Soil Bacteria Help Fight Drug-Resistant Bacteria? Soil bacteria synthesize antibiotics, which they use against species that attack or compete with them. To date, these species have been inaccessible as sources for new medicines because 99% of soil bacteria cannot be grown using standard laboratory techniques. To address this problem, researchers developed a method in which soil bacteria grow in a simulated version of their natural environment; this led to the discovery of a new antibiotic, teixobactin. In this exercise, you'll calculate means and standard errors from an experiment that tested teixobactin's effectiveness against MRSA (methicillin-resistant *Staphylococcus aureus*; see Figure 22.14).

How the Experiment Was Done Researchers drilled tiny holes into a small plastic chip and filled the holes with a dilute aqueous solution containing soil bacteria and agar. The dilution had been calibrated so that only one bacterium was likely to grow in each hole. After the agar solidified, the chip was placed in a container containing the original soil; nutrients and other essential materials from the soil diffused into the agar, allowing the bacteria to grow.

After isolating teixobactin from a soil bacterium, researchers performed the following experiment: Mice infected with MRSA were given low (1 mg/kg) or high (5 mg/kg) doses of teixobactin or vancomycin, an existing antibiotic; in the control, mice infected with MRSA were not given an antibiotic. After 26 hours, researchers sampled infected mice and estimated the number of *S. aureus* colonies in each sample. Results were reported on a log scale; note that a decrease of 1.0 on this scale reflects a tenfold decrease in MRSA abundance.

Data from the Experiment

Treatment	Dose (mg/kg)	Log of Number of Colonies	Mean ($\bar{x}$)
Control	—	9.0, 9.5, 9.0, 8.9	
Vancomycin	1.0	8.5, 8.4, 8.2	
	5.0	5.3, 5.9, 4.7	
Teixobactin	1.0	8.5, 6.0, 8.4, 6.0	
	5.0	3.8, 4.9, 5.2, 4.9	

Data from L. Ling et al. A new antibiotic kills pathogens without detectable resistance, *Nature* 517:455–459 (2015).

INTERPRET THE DATA

1. The mean ($\bar{x}$) of a variable is the sum of the data values divided by the number of observations (n):

$$\bar{x} = \frac{\sum x_i}{n}$$

In this formula, x_i is the value of the ith observation of the variable (observation number "i" out of a total of n such observations); the $\sum$ symbol indicates that the n values of x are to be added together. Calculate the mean for each treatment.

2. Use your results from question 1 to evaluate the effectiveness of vancomycin and teixobactin.
3. The variation found in a set of data can be estimated by the standard deviation, s:

$$s = \sqrt{\frac{\sum (x_i - \bar{x})^2}{n - 1}}$$

Calculate the standard deviation for each treatment.

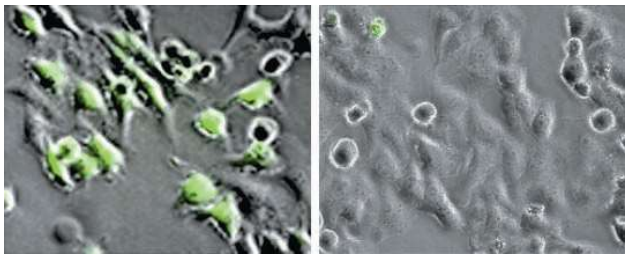
4. The standard error (SE), which indicates how greatly the mean would likely vary if the experiment was repeated, is calculated as:

$$SE = \frac{s}{\sqrt{n}}$$

As a rough rule of thumb, if an experiment were to be repeated, the new mean typically would lie within two standard errors of the original mean (that is, within the range $\bar{x} \pm 2SE$). Calculate $\bar{x} \pm 2SE$ for each treatment, determine whether these ranges overlap, and interpret your results.

Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

▼ **Figure 27.24 CRISPR: opening new avenues of research for treating HIV infection. (a)** In laboratory experiments, untreated (control) human cells were susceptible to infection by HIV, the virus that causes AIDS. **(b)** In contrast, cells treated with a CRISPR-Cas9 system that targets HIV were resistant to viral infection. The CRISPR-Cas9 system was also able to remove HIV proviruses (see Figure 19.8) that had become incorporated into the DNA of human cells.

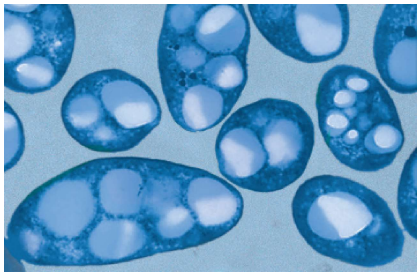


(a) Control cells. The green color indicates infection by HIV.

(b) Experimental cells. These cells were treated with a CRISPR-Cas9 system that targets HIV.

each year more than 750 billion pounds of plastic are produced from petroleum and used to make toys, storage containers, soft drink bottles, and many other items. Many of these products end up as plastic waste that contaminates natural habitats and degrades slowly, creating environmental problems (see Concept 56.4). One promising avenue for addressing these problems is to use bacteria that produce natural plastics **(Figure 27.25)**. For example, some bacteria synthesize a type of polymer known as PHA (polyhydroxyalkanoate), which they use to store chemical energy. The PHA can be extracted, formed into pellets, and used to make durable, yet biodegradable, plastics. Researchers are also seeking to reduce the use of petroleum and other fossil fuels by engineering bacteria that can produce ethanol from various forms of biomass, including agricultural waste, switchgrass, and corn.

Another way to harness prokaryotes is **bioremediation**, the use of organisms to remove pollutants from soil, air, or



◀ Figure 27.25
Bacteria synthesizing and storing PHA, a component of biodegradable plastics.

water. For example, anaerobic bacteria and archaea decompose the organic matter in sewage, converting it to material that can be used as landfill or fertilizer after chemical sterilization. Other bioremediation applications include cleaning up oil spills **(Figure 27.26)** and precipitating radioactive material (such as uranium) out of groundwater.

The usefulness of prokaryotes largely derives from their diverse forms of nutrition and metabolism. All this metabolic versatility evolved prior to the appearance of the structural novelties that heralded the evolution of eukaryotic organisms, discussed in the rest of this unit.

▶ Figure 27.26
Bioremediation of an oil spill. Spraying fertilizer stimulates the growth of native bacteria that metabolize oil, increasing the speed of the breakdown process up to fivefold.



CONCEPT CHECK 27.6

1. Identify at least two ways that prokaryotes have affected you positively today.
2. A pathogenic bacterium's toxin causes symptoms that increase the bacterium's chance of spreading from host to host. Does this information indicate whether the poison is an exotoxin or endotoxin? Explain.
3. **WHAT IF?** How might a sudden and dramatic change in your diet affect the diversity of prokaryotic species that live in your digestive tract?

For suggested answers, see Appendix A.

27 Chapter Review



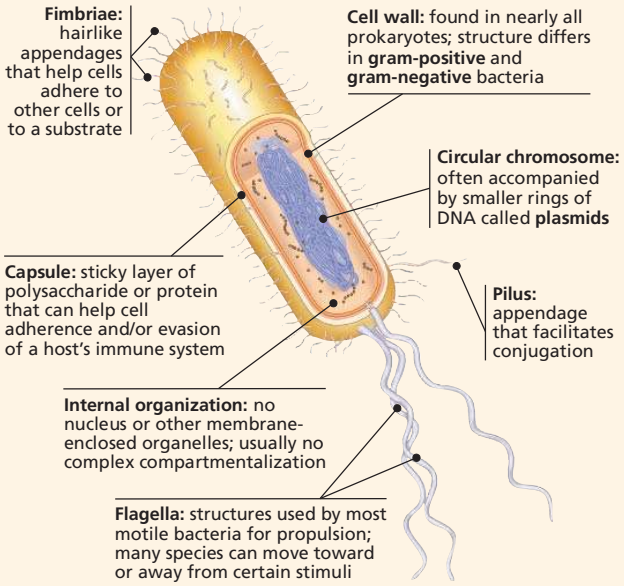
Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

CONCEPT 27.1

Structural and functional adaptations contribute to prokaryotic success *(pp. 574–578)*



- Many **prokaryotic** species can reproduce quickly by binary fission, leading to the formation of extremely large populations.

? *Describe features of prokaryotes that enable them to thrive in a wide range of different environments.*

CONCEPT 27.2

Rapid reproduction, mutation, and genetic recombination promote genetic diversity in prokaryotes *(pp. 578–581)*

- Because prokaryotes can often proliferate rapidly, mutations can quickly increase a population's genetic variation. As a result, prokaryotic populations often can evolve in short periods of time in response to changing conditions.
- Genetic diversity in prokaryotes also can arise by recombination of the DNA from two different cells (via **transformation, transduction**, or **conjugation**). By transferring advantageous alleles, such as ones for antibiotic resistance, recombination can promote adaptive evolution in prokaryotic populations.

? *Mutations are rare and prokaryotes reproduce asexually, yet their populations can have high genetic diversity. Explain how this can occur.*

CONCEPT 27.3

Diverse nutritional and metabolic adaptations have evolved in prokaryotes *(pp. 581–583)*

- Nutritional diversity is much greater in prokaryotes than in eukaryotes and includes all four modes of nutrition: photoautotrophy, chemoautotrophy, photoheterotrophy, and chemoheterotrophy.
- Among prokaryotes, **obligate aerobes** require O_2, **obligate anaerobes** are poisoned by O_2, and **facultative anaerobes** can survive with or without O_2.

- Unlike eukaryotes, prokaryotes can metabolize nitrogen in many different forms. Some can convert atmospheric nitrogen to ammonia, a process called **nitrogen fixation**.
- Prokaryotic cells and even species may cooperate metabolically, including in surface-coating **biofilms**.

? *Describe the range of prokaryotic metabolic adaptations.*

CONCEPT 27.4

Prokaryotes have radiated into a diverse set of lineages *(pp. 583–586)*

- Molecular systematics is helping biologists classify prokaryotes and identify new clades.
- Diverse nutritional types are scattered among the major groups of bacteria. The two largest groups are proteobacteria and gram-positive bacteria.
- Some archaea, such as **extreme thermophiles** and **extreme halophiles**, live in extreme environments. Other archaea live in moderate environments such as soils and lakes.

? *How have molecular data informed prokaryotic phylogeny?*

CONCEPT 27.5

Prokaryotes play crucial roles in the biosphere *(pp. 586–587)*

- Decomposition by heterotrophic prokaryotes and the synthetic activities of autotrophic and nitrogen-fixing prokaryotes contribute to the recycling of elements in ecosystems.
- Many prokaryotes have a **symbiotic** relationship with a **host**; the relationships between prokaryotes and their hosts range from **mutualism** to **commensalism** to **parasitism**.

? *In what ways are prokaryotes key to the survival of many species?*

CONCEPT 27.6

Prokaryotes have both beneficial and harmful impacts on humans *(pp. 587–591)*

- People depend on mutualistic prokaryotes, including hundreds of species that live in our intestines and help digest food.
- Pathogenic bacteria typically cause disease by releasing **exotoxins** or **endotoxins**. Horizontal gene transfer can spread genes associated with virulence to harmless species or strains.
- Resistance to multiple antibiotics has evolved in many pathogenic bacteria, a problem of great concern for public health.
- Prokaryotes can be used in **bioremediation** and production of plastics, vitamins, antibiotics, and other products.

? *Describe beneficial and harmful impacts of prokaryotes on humans.*

TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

1. A process that cannot produce genetic variation in bacterial populations is
   (A) transduction. (C) mutation.
   (B) conjugation. (D) meiosis.
2. Photoautotrophs use
   (A) light as an energy source and CO_2 as a carbon source.
   (B) light as an energy source and methane as a carbon source.
   (C) N_2 as an energy source and CO_2 as a carbon source.
   (D) CO_2 as both an energy source and a carbon source.
3. Which of the following statements is true?
   (A) Archaea and bacteria have identical membrane lipids.
   (B) The cell walls of archaea lack peptidoglycan.
   (C) Prokaryotes have low levels of genetic diversity.
   (D) No archaea are capable of using CO_2 to oxidize H_2, releasing methane.
4. Which of the following involves metabolic cooperation among prokaryotic cells?
   (A) binary fission (C) biofilms
   (B) endospore formation (D) photoautotrophy
5. Which of the following describes a bacterium that lives in the human intestine and causes disease?
   (A) commensalist (C) gut mutualist
   (B) decomposer (D) symbiotic pathogen
6. Photosynthesis that releases O_2 occurs in
   (A) cyanobacteria. (C) gram-positive bacteria.
   (B) archaea. (D) chemoautotrophic bacteria.

Levels 3-4: Applying/Analyzing

7. **EVOLUTION CONNECTION** In patients with nonresistant strains of the tuberculosis bacterium, antibiotics can relieve symptoms in a few weeks. However, it takes much longer to halt the infection, and patients may discontinue treatment while bacteria are still present. Explain how this could result in the evolution of drug-resistant pathogens.

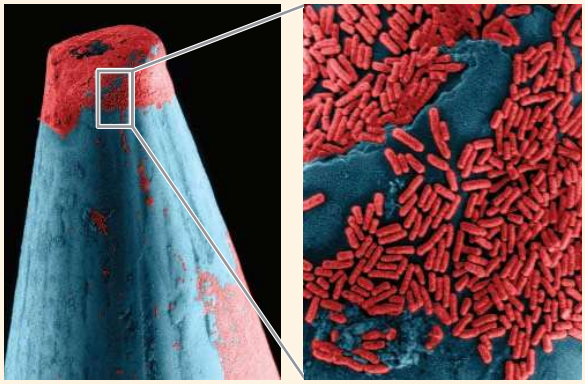
Levels 5-6: Evaluating/Creating

8. **SCIENTIFIC INQUIRY • INTERPRET THE DATA** The nitrogen-fixing bacterium *Rhizobium* infects the roots of some plant species, forming a mutualism in which the bacterium provides nitrogen, and the plant provides carbohydrates. Scientists measured the 12-week growth of one such plant species (*Acacia irrorata*) when infected by six different *Rhizobium* strains. (a) Graph the data. (b) Interpret the graph.

Rhizobium strain	1	2	3	4	5	6
Plant mass (g)	0.91	0.06	1.56	1.72	0.14	1.03

Data from J. J. Burdon et al., Variation in the effectiveness of symbiotic associations between native rhizobia and temperate Australian *Acacia*: within species interactions, *Journal of Applied Ecology* 36:398–408 (1999).
Note: Without *Rhizobium*, after 12 weeks, *Acacia* plants have a mass of about 0.1 g.

9. **WRITE ABOUT A THEME: ENERGY** In a short essay (about 100–150 words), discuss how prokaryotes and other members of hydrothermal vent communities transfer and transform energy.
10. **SYNTHESIZE YOUR KNOWLEDGE**



Explain how the small size and rapid reproduction rate of bacteria (such as the population shown here on the tip of a pin) contribute to their large population sizes and high genetic variation.

For selected answers, see Appendix A.

28 Protists

KEY CONCEPTS

28.1 Most eukaryotes are single-celled organisms *p. 594*

28.2 Excavates include protists with modified mitochondria and protists with unique flagella *p. 597*

28.3 SAR is a highly diverse group of protists defined by DNA similarities *p. 601*

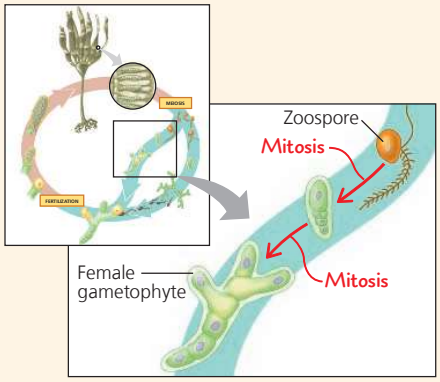
28.4 Red algae and green algae are the closest relatives of plants *p. 609*

28.5 Unikonts include protists that are closely related to fungi and animals *p. 611*

28.6 Protists play key roles in ecological communities *p. 614*

Study Tip

Label a drawing: Protist life cycles vary greatly. To make sense of this variation, it can be helpful to identify when mitosis occurs in different life cycles, as shown here for a portion of Figure 28.14. Identify the stages at which mitosis occurs in Figures 28.14, 28.18, 28.25, and 28.28.



Go to Mastering Biology

For Students (in eText and Study Area)
- Get Ready for Chapter 28
- Animation: Life Cycle of a Malaria Parasite

For Instructors to Assign (in Item Library)
- Scientific Skills Exercise: Interpreting Comparisons of Genetic Sequences
- Misconception Questions 136–140

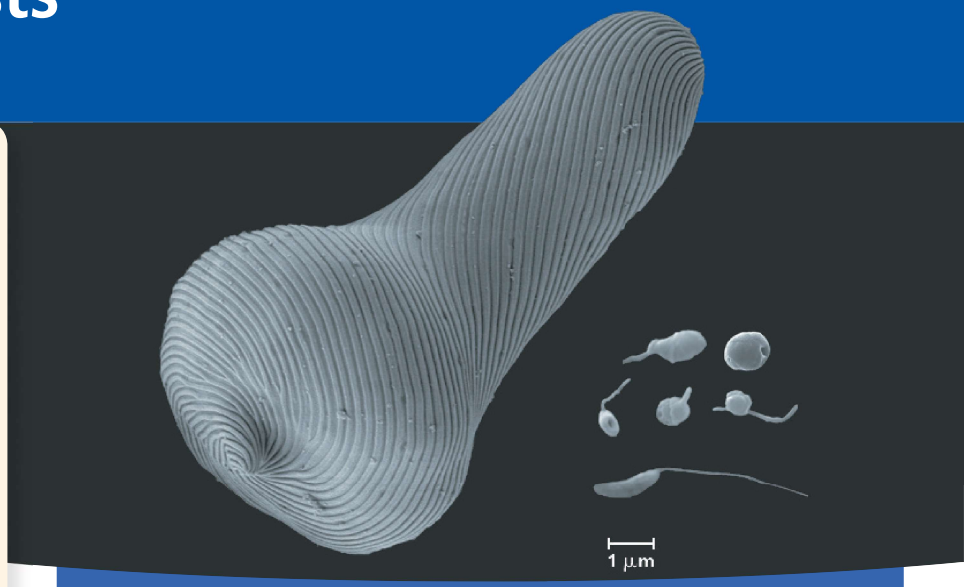
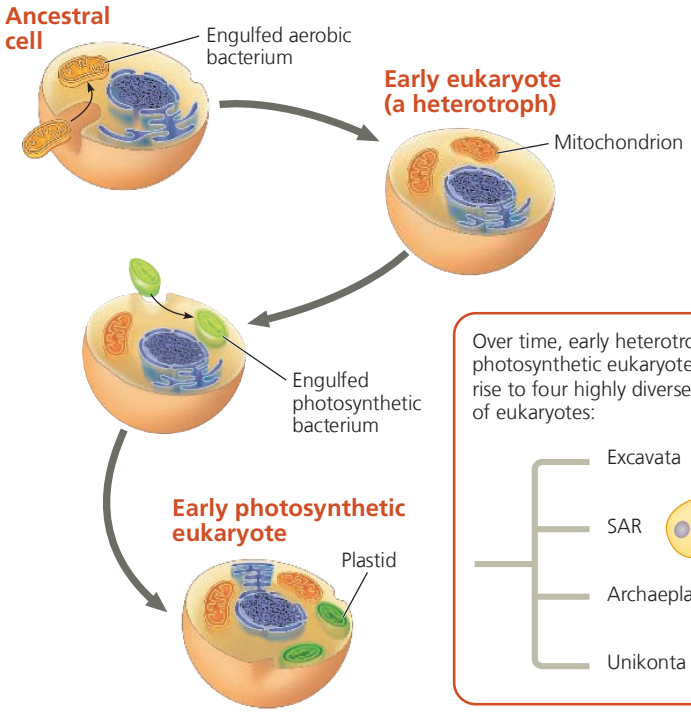


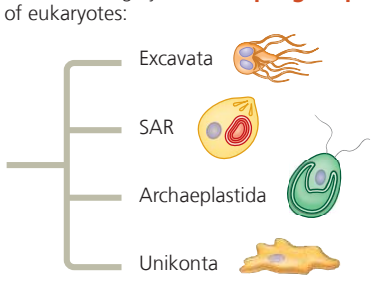
Figure 28.1 Knowing that prokaryotes are extremely small, you might assume that this image shows six prokaryotes and one much larger eukaryote. But in fact, the only prokaryote is the organism immediately above the scale bar—the rest are members of diverse, mostly unicellular groups of eukaryotes informally known as **protists**.

What gave rise to the great diversity of protists, and how have their lineages diverged over time?

Much of protistan diversity can be traced to **endosymbiosis:**



Over time, early heterotrophic and photosynthetic eukaryotes have given rise to four highly diverse **supergroups** of eukaryotes:



CONCEPT 28.1

Most eukaryotes are single-celled organisms

Protists—along with plants, animals, and fungi—are eukaryotes; they are in domain Eukarya, one of the three domains of life. Genetic and morphological studies have shown that some protists are more closely related to plants, fungi, or animals than they are to other protists. As a result, the kingdom in which all protists once were classified, Protista, has been abandoned, and various protist lineages are now recognized as major groups in their own right. Most biologists still use the term *protist*, but only as a convenient way to refer to eukaryotes that are not plants, animals, or fungi.

Unlike the cells of prokaryotes, the cells of protists and other eukaryotes have a nucleus and other membrane-enclosed organelles, such as mitochondria and the Golgi apparatus. Such organelles provide specific locations where particular cellular functions are accomplished, making the structure and organization of eukaryotic cells more complex than those of prokaryotic cells. Eukaryotic cells also have a well-developed cytoskeleton that extends throughout the cell (see Figure 6.20). The cytoskeleton provides the structural support that enables eukaryotic cells to have asymmetric (irregular) forms, as well as to change in shape as they feed, move, or grow. In contrast, prokaryotic cells lack a well-developed cytoskeleton, thus limiting the extent to which they can maintain asymmetric forms or change shape over time.

We'll survey the diversity of eukaryotes throughout the rest of this unit, beginning in this chapter with the protists. As you explore this material, bear in mind that

- the organisms in most eukaryotic lineages are protists, and
- most protists are unicellular.

Thus, life differs greatly from how most of us commonly think of it. The large, multicellular organisms that we know best (plants, animals, and fungi) are the tips of just a few branches on the great tree of life (see Figure 26.21).

Mastering Biology **HHMI Video: Seeing the Invisible: Van Leeuwenhoek's First Glimpses of the Microbial World**

Structural and Functional Diversity in Protists

Given that they are classified in a number of different groups, it isn't surprising that few general characteristics of protists can be cited without exceptions. In fact, protists exhibit more structural and functional diversity than the eukaryotes with which we are most familiar—plants, animals, and fungi.

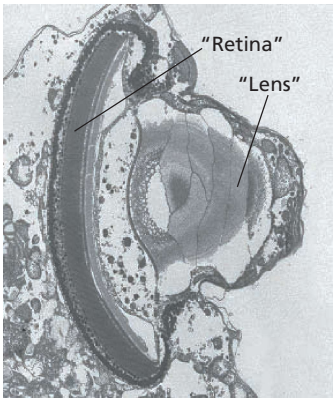
For example, most protists are unicellular, although there are some colonial and multicellular species. Single-celled protists are justifiably considered the simplest eukaryotes, but at the cellular level, many protists are very complex—the most elaborate of all cells. In multicellular organisms, essential biological functions are carried out by organs. Unicellular protists carry out the same essential functions, but they do so using subcellular organelles, not multicellular organs. The organelles that protists use are mostly those discussed in Figure 6.8, including the nucleus, endoplasmic reticulum, Golgi apparatus, and lysosomes. Certain protists also rely on organelles not found in most other eukaryotic cells, such as contractile vacuoles that pump excess water from the protistan cell (see Figure 7.13). One group of dinoflagellate protists has the most complex subcellular structure known: a unique, eye-like organelle called an *ocelloid* with components resembling the lens and retina in the eyes of vertebrates and some other animals **(Figure 28.2)**.

Protists are also very diverse in their nutrition. Some protists are photoautotrophs and contain chloroplasts. Some are heterotrophs, absorbing organic molecules or ingesting larger food particles. Still other protists, called **mixotrophs**, combine photosynthesis and heterotrophic nutrition. Photoautotrophy, heterotrophy, and mixotrophy have all arisen independently in many different protist lineages.

Reproduction and life cycles also are highly varied among protists. Some protists are only known to reproduce asexually; others can also reproduce sexually or at least employ the sexual processes of meiosis and fertilization. All three basic types of sexual life cycles (see Figure 13.6) are represented among protists, along with some variations that do not quite fit any of these types. We will examine the life cycles of several protist groups later in this chapter.

Endosymbiosis in Eukaryotic Evolution

What gave rise to the enormous diversity of protists that exist today? There is abundant evidence that much of protistan diversity has its origins in **endosymbiosis**, a relationship



▶ Figure 28.2 The eye-like ocelloid of *Erythropsidinium*, a dinoflagellate. This complex, subcellular structure resembles the camera-like eye found in vertebrates and some molluscs. In some dinoflagellates, the ocelloid may function in prey detection.

between two species in which one organism lives inside the cell or cells of another organism (the host). In particular, as we discussed in Concept 25.3, structural, biochemical, and DNA sequence data indicate that mitochondria and plastids are derived from bacteria that were engulfed by the ancestors of early eukaryotic cells. The evidence also suggests that mitochondria evolved before plastids. Thus, a defining moment in the origin of eukaryotes occurred when a host cell engulfed a bacterium that would later become an organelle found in all eukaryotes—the mitochondrion.

To determine which bacterial lineage gave rise to mitochondria, researchers have compared the DNA sequences of mitochondrial genes (mtDNA) to those found in major clades of bacteria. In the **Scientific Skills Exercise**, you will interpret one such set of DNA sequence comparisons. Collectively, such studies indicate that mitochondria arose from an alpha proteobacterium (see Figure 27.17). Results from mtDNA sequence analyses also indicate that the mitochondria of protists, animals, fungi, and plants descended from a single common ancestor, thus suggesting that mitochondria arose only once over the course of evolution. Similar analyses provide evidence that plastids descended from a single common ancestor—a cyanobacterium that was engulfed by a eukaryotic host cell.

Scientific Skills Exercise

Interpreting Comparisons of Genetic Sequences

Which Bacteria Are Most Closely Related to Mitochondria? Early eukaryotes acquired mitochondria by endosymbiosis: A host cell engulfed an aerobic bacterium that persisted within the cytoplasm to the mutual benefit of both cells. In studying which living bacteria might be most closely related to mitochondria, researchers compared DNA sequences encoding ribosomal RNA (rRNA), a component of ribosomes. Ribosomes perform critical cell functions. Hence, genes encoding rRNA are under strong selection and change slowly over time, making them suitable for comparing even distantly related species. In this exercise, you will interpret some of the research data to draw conclusions about the phylogeny of mitochondria.

How the Research Was Done Researchers isolated and cloned DNA sequences from the gene that codes for the small-subunit rRNA molecule for the wheat (a eukaryote) mitochondrion and for five bacterial species:

- Wheat, used as the source of genes encoding mitochondrial rRNA
- *Agrobacterium tumefaciens*, an alpha proteobacterium that lives within plant tissue and produces tumors in the host
- *Comamonas testosteroni*, a beta proteobacterium
- *Escherichia coli*, a well-studied gamma proteobacterium that inhabits human intestines
- *Mycoplasma capricolum*, a gram-positive mycoplasma, which is the only group of bacteria lacking cell walls
- *Anacystis nidulans,* a cyanobacterium

Data from the Research Gene sequences encoding rRNA for the wheat mitochondrion and the five bacteria were aligned and compared. The data table below, called a *comparison matrix*, summarizes the comparison of 617 nucleotide positions from the gene sequences. Each value in the table is the percentage of the 617 nucleotide positions for which the pair of organisms have the same base. Any positions that were identical across all six RNA-encoding gene sequences were omitted from this comparison matrix.



▶ **Wheat, used as the source of mitochondrial RNA**

INTERPRET THE DATA

1. First, make sure you understand how to read the comparison matrix. **(a)** Find the cell that represents the comparison of *C. testosteroni* and *E. coli*. What value is given in this cell? **(b)** What does that value signify about the comparable gene sequences in those two organisms? **(c)** Explain why some cells have a dash rather than a value. **(d)** Why are some cells shaded gray, with no value?
2. Why did the researchers choose one plant mitochondrion and five bacterial species to include in the comparison matrix?
3. **(a)** Which bacterium has an rRNA-encoding gene that is most similar to that of the wheat mitochondrion? **(b)** What is the significance of this similarity?

Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

	Wheat mitochondrion	*A. tumefaciens*	*C. testosteroni*	*E. coli*	*M. capricolum*	*A. nidulans*
Wheat mitochondrion	–	48	38	35	34	34
A. tumefaciens		–	55	57	52	53
C. testosteroni			–	61	52	52
E. coli				–	48	52
M. capricolum					–	50
A. nidulans						–

Data from D. Yang et al., Mitochondrial origins, *Proceedings of the National Academy of Sciences USA* 82:4443–4447 (1985).

Progress has also been made toward identifying the host cell that engulfed an alpha proteobacterium, thereby setting the stage for the origin of eukaryotes. For example, researchers recently reported the discovery of a new group of archaea, the lokiarchaeotes. In phylogenomic analyses, this group was identified as the sister group of the eukaryotes and its genome was found to encode many eukaryote-specific features. Was the host cell that engulfed an alpha proteobacterium a lokiarchaeote? While this could be correct, it is also possible that the host belonged to a different lineage of archaea or was closely related to the archaea (but was not itself an archaean). In any case, current evidence indicates that the host was a relatively complex cell in which certain features of eukaryotic cells had evolved, such as a cytoskeleton that enabled it to change shape (and thereby engulf the alpha proteobacterium).

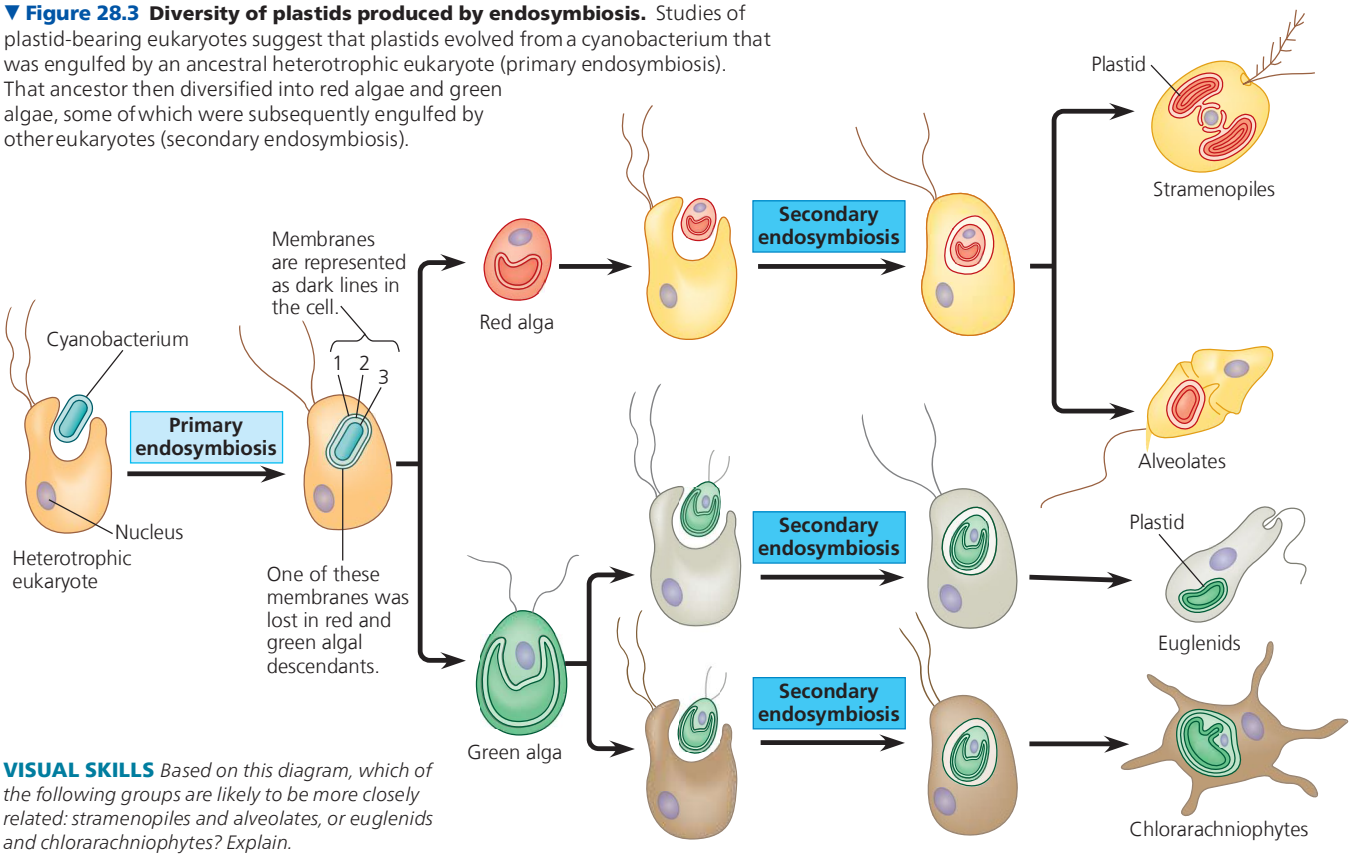
Plastid Evolution: A Closer Look

As you've seen, current evidence indicates that mitochondria are descended from a bacterium that was engulfed by a host cell that was an archaean (or a close relative of the archaea). This event gave rise to the eukaryotes. There is also much evidence that later in eukaryotic history, a lineage of heterotrophic eukaryotes acquired an additional endosymbiont—a photosynthetic cyanobacterium—that then evolved into plastids. According to the hypothesis illustrated in **Figure 28.3**, this plastid-bearing lineage gave rise to two lineages of photosynthetic protists, or **algae**: red algae and green algae.

Let's examine some of the steps in Figure 28.3 more closely. First, recall that cyanobacteria are gram-negative and that gram-negative bacteria have two cell membranes, an inner plasma membrane and an outer membrane that is part of the cell wall (see Figure 27.3). Plastids in red algae and green algae are also surrounded by two membranes. Transport proteins in these membranes are homologous to proteins in the inner and outer membranes of cyanobacteria, providing further support for the hypothesis that plastids originated from a cyanobacterial endosymbiont.

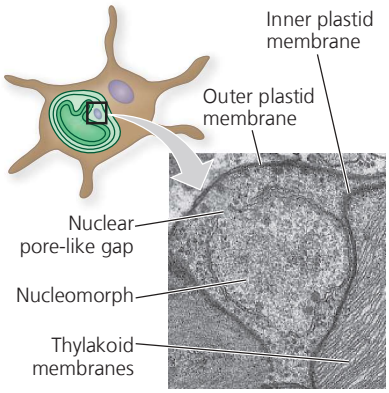
On several occasions during eukaryotic evolution, red algae and green algae underwent **secondary endosymbiosis**, meaning they were ingested in the food vacuoles of heterotrophic eukaryotes and became endosymbionts themselves. For example, protists known as chlorarachniophytes likely evolved when a heterotrophic eukaryote engulfed a green alga. Evidence for this process can be found within the

▼ Figure 28.3 Diversity of plastids produced by endosymbiosis. Studies of plastid-bearing eukaryotes suggest that plastids evolved from a cyanobacterium that was engulfed by an ancestral heterotrophic eukaryote (primary endosymbiosis). That ancestor then diversified into red algae and green algae, some of which were subsequently engulfed by other eukaryotes (secondary endosymbiosis).



VISUAL SKILLS *Based on this diagram, which of the following groups are likely to be more closely related: stramenopiles and alveolates, or euglenids and chlorarachniophytes? Explain.*

▶ Figure 28.4 Nucleomorph within a plastid of a chlorarachniophyte.



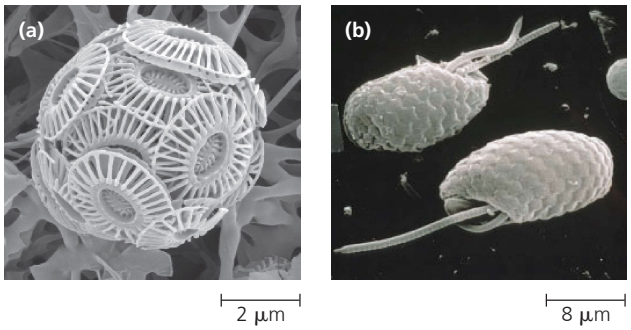
engulfed cell, which contains a tiny vestigial nucleus, called a *nucleomorph* **(Figure 28.4)**. Genes from the nucleomorph are still transcribed, and their DNA sequences indicate that the engulfed cell was a green alga.

Four Supergroups of Eukaryotes

Our understanding of the evolutionary history of eukaryotic diversity has been in flux in recent years. Not only has kingdom Protista been abandoned, but other hypotheses have been discarded as well. For example, many biologists once thought that the first lineage to have diverged from all other eukaryotes was the *amitochondriate protists*, organisms without conventional mitochondria and with fewer membrane-enclosed organelles than other protist groups. But recent structural and DNA data have undermined this hypothesis. Many of the so-called amitochondriate protists have been shown to have mitochondria—though reduced ones—and some of these organisms are now classified in distantly related groups.

The ongoing changes in our understanding of the phylogeny of protists pose challenges to students and instructors alike. Hypotheses about these relationships are a focus of scientific activity, changing rapidly as new data cause previous ideas to be modified or discarded. We'll focus here on one current hypothesis: the four supergroups of eukaryotes shown in **Figure 28.5**. Because the root of the eukaryotic tree is not known, all four supergroups are shown as diverging simultaneously from a common ancestor. We know that this is not correct, but we do not know which supergroup was the first to diverge from the other three. In addition, major new groups of protists have been discovered in recent years, but their relationship to the supergroups shown in Figure 28.5 has yet to be resolved. Examples of such unresolved groups include haptophytes and cryptophytes **(Figure 28.6)**, as well as the hemimastigophores, a novel group described in 2018. Overall, as you read this chapter, it may be helpful to focus less on the specific names of groups of organisms and more on why the organisms are important and how ongoing research is elucidating their evolutionary relationships.

▼ Figure 28.6 A haptophyte and a cryptophyte. Although they are major groups of protists, haptophytes and cryptophytes are not shown in Figure 28.5 because their phylogenetic relationships have yet to be resolved. **(a)** The haptophyte *Emiliania huxleyi* is a key producer in the ocean. **(b)** The outer surface of this photosynthetic cryptophyte is covered with protective plates. (SEM)



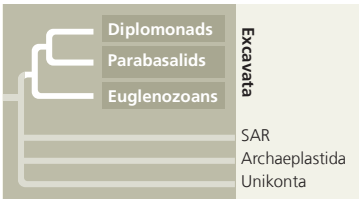
CONCEPT CHECK 28.1

1. Cite at least four examples of structural and functional diversity among protists.
2. Summarize the role of endosymbiosis in eukaryotic evolution.
3. **MAKE CONNECTIONS** After studying Figure 28.3, predict how many distinct genomes are contained within the cell of a chlorarachniophyte. Explain. (See Figures 6.17 and 6.18.)

For suggested answers, see Appendix A.

CONCEPT 28.2

Excavates include protists with modified mitochondria and protists with unique flagella

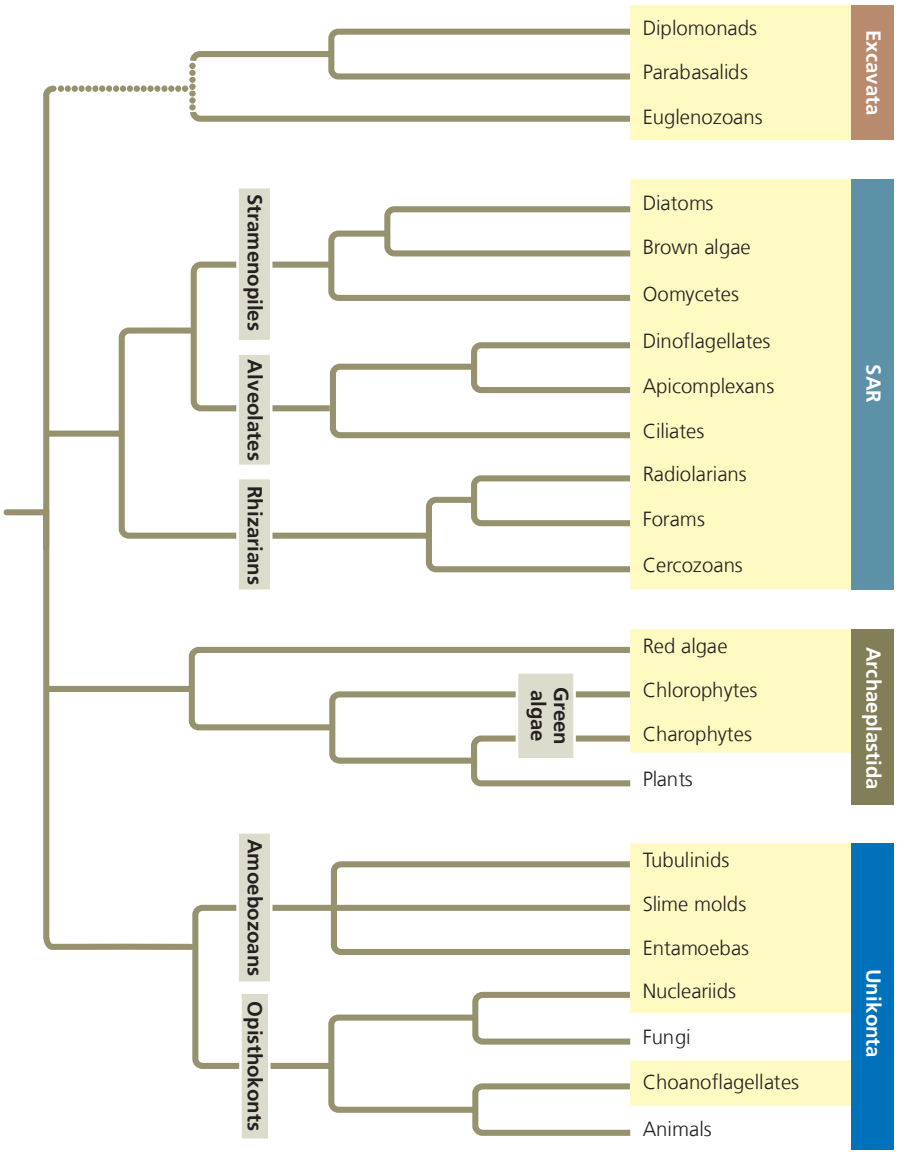


Now that we have examined some of the broad patterns in eukaryotic evolution, we will look more closely at the four main groups of protists shown in Figure 28.5.

We begin with **Excavata** (the excavates), a clade that was originally proposed based on morphological studies of the

▼ Figure 28.5 Exploring Protistan Diversity

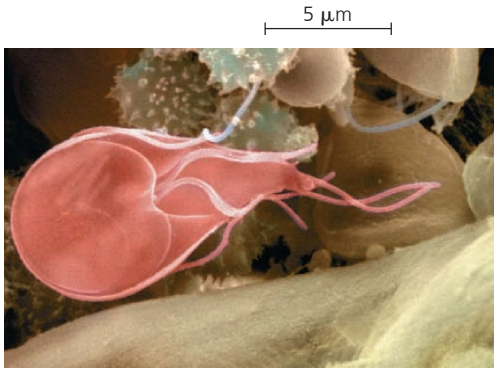
The tree below represents a phylogenetic hypothesis for the relationships among eukaryotes on Earth today. The eukaryotic groups at the branch tips are related in larger "supergroups," labeled vertically at the far right of the tree. Groups that were formerly classified in the kingdom Protista are highlighted in yellow. Dotted lines indicate evolutionary relationships that are uncertain. For clarity, this tree only includes representative clades from each supergroup. In addition, the recent discoveries of many new groups of eukaryotes indicate that eukaryotic diversity is actually much greater than shown here.



DRAW IT *Draw a simplified version of this phylogenetic tree that shows only the four supergroups of eukaryotes. Now sketch how the tree would look if the unikonts were the sister group to all other eukaryotes.*

Excavata

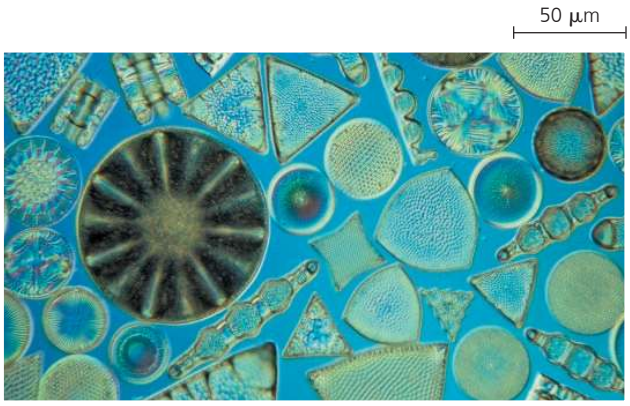
Some members of this supergroup (whose monophyly has been called into question by some recent genomic studies) have an "excavated" groove on one side of the cell body. Two major clades (the parabasalids and diplomonads) have highly reduced mitochondria; members of a third clade (the euglenozoans) have flagella that differ in structure from those of other organisms. Excavates include parasites such as *Giardia*, as well as many predatory and photosynthetic species.



***Giardia intestinalis*, a diplomonad parasite.** This diplomonad (colorized SEM), which lacks the characteristic surface groove of the Excavata, inhabits the intestines of mammals. It can infect people when they drink water contaminated with feces containing *Giardia* cysts. Drinking such water—even from a seemingly pristine stream—can cause severe diarrhea. Boiling the water kills the parasite.

SAR

This supergroup contains (and is named after) three large and very diverse clades: Stramenopila, Alveolata, and Rhizaria. Stramenopiles include some of the most important photosynthetic organisms on Earth, such as the diatoms shown here. Alveolates also include photosynthetic species, as well as important pathogens, such as *Plasmodium*, which causes malaria. According to one current hypothesis, stramenopiles and alveolates originated by secondary endosymbiosis when a heterotrophic protist engulfed a red alga.



Diatom diversity. These beautiful single-celled protists are important photosynthetic organisms in aquatic communities (LM).

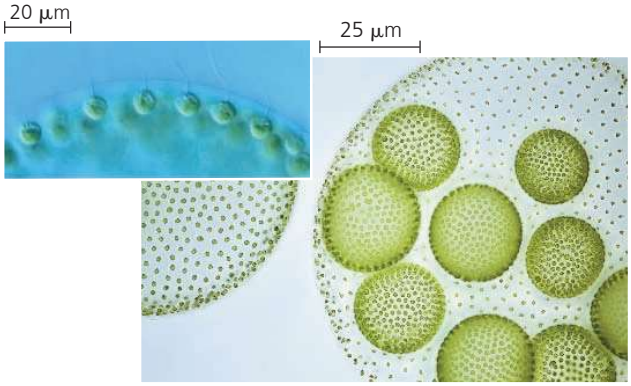
The rhizarian subgroup of SAR includes many species of amoebas, most of which have pseudopodia that are threadlike in shape. Pseudopodia are extensions that can bulge from any portion of the cell; they are used in movement and in the capture of prey.



***Globigerina*, a rhizarian in SAR.** This species is a foram, a group whose members have threadlike pseudopodia that extend through pores in the shell, or test (LM). The inset shows a foram test, which is hardened by calcium carbonate.

Archaeplastida

This supergroup of eukaryotes includes red algae and green algae, along with plants. Red algae and green algae include unicellular species, colonial species, and multicellular species (including the green alga *Volvox*). Many of the large algae known informally as "seaweeds" are multicellular red or green algae. Protists in Archaeplastida include key photosynthetic species that form the base of the food web in many aquatic communities.



***Volvox*, a multicellular freshwater green alga.** This alga has two types of differentiated cells, and so it is considered multicellular rather than colonial. It resembles a hollow ball whose wall is composed of hundreds of biflagellated cells (see inset LM) embedded in a gelatinous extracellular matrix; if isolated, these cells cannot reproduce. However, the alga also contains cells that are specialized for either sexual or asexual reproduction. The large algae shown here will eventually release the small "daughter" algae that can be seen within them (LM).

Mastering Biology Video: ***Volvox***

Unikonta

This supergroup of eukaryotes, also called Amorphea, includes amoebas that have lobe- or tube-shaped pseudopodia, as well as animals, fungi, and non-amoeba protists that are closely related to animals or fungi. According to one current hypothesis, the unikonts were the first eukaryotic supergroup to diverge from all other eukaryotes; however, this hypothesis has yet to be widely accepted.



A unikont amoeba. This amoeba, the tubulinid *Amoeba proteus*, is using its pseudopodia to move.

Mastering Biology Video: ***Amoeba* Pseudopodium**

cytoskeleton. Some members of this diverse group also have an "excavated" feeding groove on one side of the cell body. The excavates include the diplomonads, parabasalids, and euglenozoans. Molecular data indicate that each of these three groups is monophyletic. In contrast, some recent genomic studies indicate that the excavates are not monophyletic, making Excavata the most controversial of our four supergroups.

Diplomonads and Parabasalids

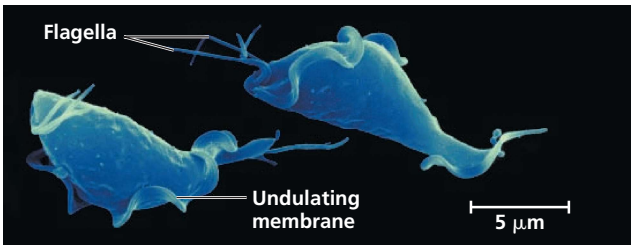
The protists in these two groups lack plastids and have highly reduced mitochondria (until recently, they were thought to lack mitochondria altogether). Most diplomonads and parabasalids are found in anaerobic environments.

Diplomonads have reduced mitochondria called *mitosomes*. These organelles lack functional electron transport chains and hence cannot use oxygen to help extract energy from carbohydrates and other organic molecules. Instead, diplomonads get the energy they need from anaerobic biochemical pathways. Many diplomonads are parasites, including the infamous *Giardia intestinalis* (see Figure 28.5), which inhabits the intestines of mammals.

Structurally, diplomonads have two equal-sized nuclei and multiple flagella. Recall that eukaryotic flagella are extensions of the cytoplasm, consisting of bundles of microtubules covered by the cell's plasma membrane (see Figure 6.24). They are quite different from prokaryotic flagella, which are filaments composed of globular proteins attached to the cell surface (see Figure 27.7).

Parabasalids also have reduced mitochondria; called *hydrogenosomes*, these organelles generate some energy anaerobically, releasing hydrogen gas as a by-product. The best-known parabasalid is *Trichomonas vaginalis*, a sexually transmitted parasite that infects about 140 million people each year worldwide. *T. vaginalis* travels along the mucus-coated lining of the human reproductive and urinary tracts by moving its flagella and by undulating part of its plasma membrane **(Figure 28.7)**. In females, if the vagina's normal acidity is disturbed, *T. vaginalis* can outcompete beneficial microorganisms there and infect the vagina. One of *T. vaginalis*'s genes encodes a product that allows it to feed on the vaginal lining, promoting infection. Studies suggest that *T. vaginalis* acquired this gene by horizontal gene transfer from bacterial parasites in the vagina. (*Trichomonas* infections also can occur in the urethra of males, though often without symptoms.)

▼ Figure 28.7 The parabasalid parasite *Trichomonas vaginalis*. (colorized SEM)



Euglenozoans

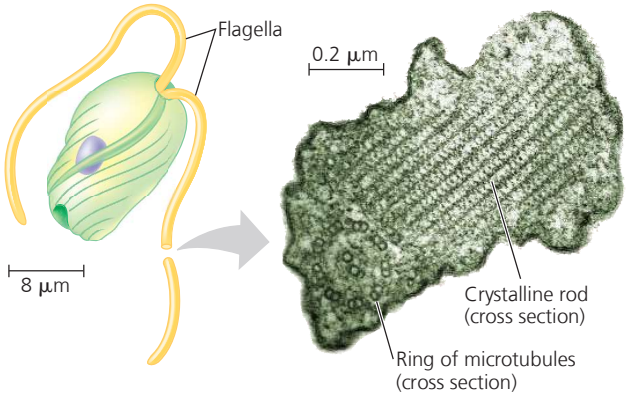
Protists called **euglenozoans** belong to a diverse clade that includes predatory heterotrophs, photosynthetic autotrophs, mixotrophs, and parasites. The main morphological feature that distinguishes protists in this clade is the presence of a rod with either a spiral or a crystalline structure inside each of their flagella **(Figure 28.8)**. The two best-studied groups of euglenozoans are the kinetoplastids and the euglenids.

Kinetoplastids

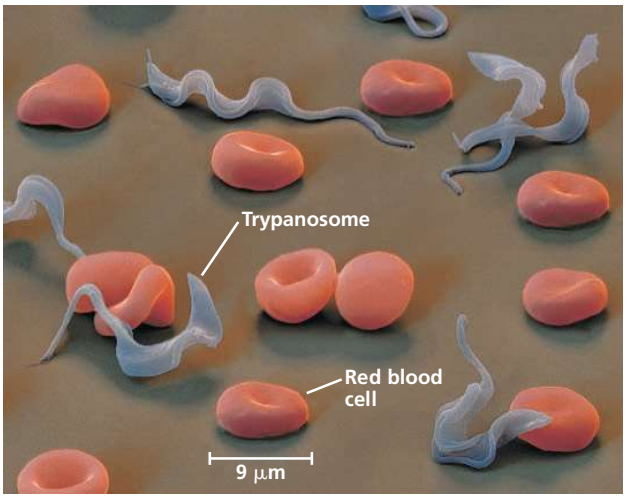
Protists called **kinetoplastids** have a single, large mitochondrion that contains an organized mass of DNA called a *kinetoplast*. These protists include species that feed on prokaryotes in freshwater, marine, and moist terrestrial ecosystems, as well as species that parasitize animals, plants, and other protists. For example, kinetoplastids in the genus *Trypanosoma* infect humans and cause sleeping sickness **(Figure 28.9)**, a neurological disease that is invariably fatal if not treated. This disease currently afflicts about 10,000 people each year, mostly in rural areas of Africa. The infection occurs via the bite of a vector (carrier) organism, the African tsetse fly. Trypanosomes also cause Chagas' disease, which is transmitted by bloodsucking insects and can lead to congestive heart failure.

Trypanosomes evade immune responses with an effective "bait-and-switch" defense. The surface of a trypanosome is coated with millions of copies of a single protein. However, before the host's immune system can recognize the protein and mount an attack, new generations of the

▼ Figure 28.8 Euglenozoan flagellum. Most euglenozoans have a crystalline rod inside one of their flagella (the TEM is a flagellum shown in cross section). The rod lies alongside the 9 + 2 ring of microtubules found in all eukaryotic flagella (compare with Figure 6.24).



▼ Figure 28.9 *Trypanosoma*, the kinetoplastid that causes sleeping sickness. (colorized SEM)



parasite switch to another surface protein with a different molecular structure. Frequent changes in the surface protein prevent the host from developing immunity. (The Scientific Skills Exercise in Chapter 43 explores this topic further.) About a third of *Trypanosoma*'s genome is dedicated to producing these surface proteins.

Euglenids

A **euglenid** has a pocket at one end of the cell from which one or two flagella emerge **(Figure 28.10)**. Some euglenids are mixotrophs: They perform photosynthesis when sunlight is available, but when it is not, they can become heterotrophic, absorbing organic nutrients from their environment. Many other euglenids engulf prey by phagocytosis.

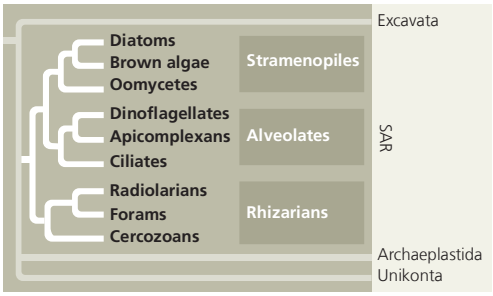
CONCEPT CHECK 28.2

1. Why do some biologists describe the mitochondria of diplomonads and parabasalids as "highly reduced"?
2. **WHAT IF?** DNA sequence data for a diplomonad, a euglenid, a plant, and an unidentified protist suggest that the unidentified species is most closely related to the diplomonad. Further studies reveal that the unknown species has fully functional mitochondria. Based on these data, at what point on the phylogenetic tree in Figure 28.5 did the mystery protist's lineage probably diverge from other eukaryote lineages? Explain.

For suggested answers, see Appendix A.

CONCEPT 28.3

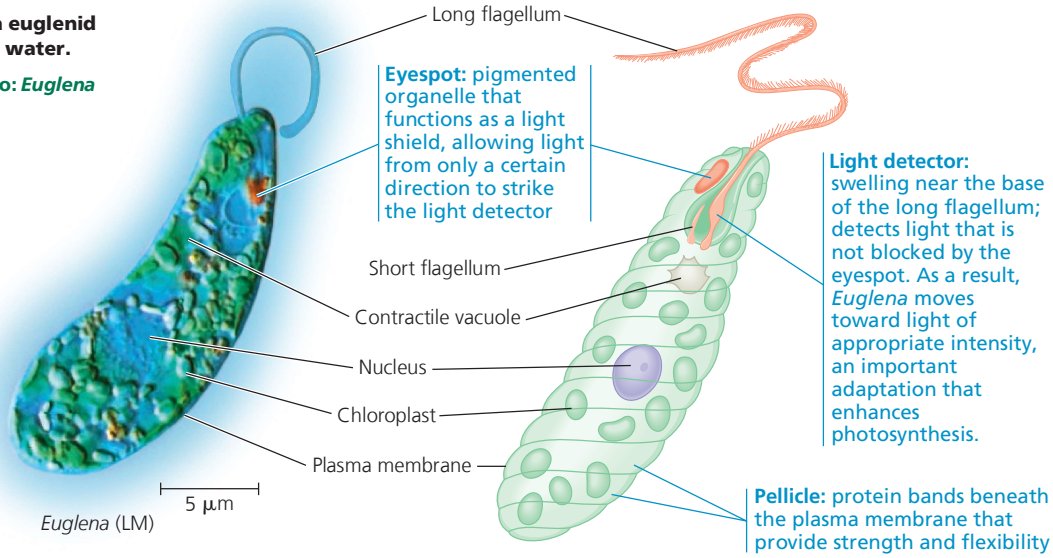
SAR is a highly diverse group of protists defined by DNA similarities



Our second supergroup, referred to as **SAR**, was proposed recently based on whole-genome DNA sequence analyses. These studies found that three major clades of protists—the stramenopiles, alveolates, and rhizarians—form a monophyletic supergroup. This supergroup contains a large, extremely diverse collection of protists. To date, this supergroup has not

▶ Figure 28.10 *Euglena*, a euglenid commonly found in pond water.

Mastering Biology **Video: *Euglena***



received a formal name but is instead known by the first letters of its major clades: SAR.

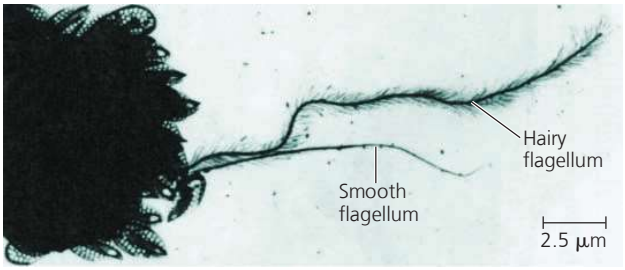
Some morphological and DNA sequence data suggest that two of these groups, the stramenopiles and alveolates, originated more than a billion years ago, when a common ancestor of these two clades engulfed a single-celled, photosynthetic red alga. Because red algae are thought to have originated by primary endosymbiosis (see Figure 28.3), such an origin for the stramenopiles and alveolates is referred to as secondary endosymbiosis. Others question this idea, noting that some species in these groups lack plastids or their remnants (including any trace of plastid genes in their nuclear DNA).

Despite its lack of a formal name, the SAR supergroup represents the best current hypothesis for the phylogeny of the three large protist clades to which we now turn.

Stramenopiles

One major subgroup of SAR, the **stramenopiles**, includes some of the most important photosynthetic organisms on the planet. Their name (from the Latin *stramen*, straw, and *pilos*, hair) refers to their characteristic flagellum, which has numerous fine, hairlike projections. In most stramenopiles, this "hairy" flagellum is paired with a shorter "smooth" (nonhairy) flagellum **(Figure 28.11)**. Here we'll focus on three groups of stramenopiles: diatoms, oomycetes, and brown algae.

▼ Figure 28.11 Stramenopile flagella. Most stramenopiles, such as *Synura petersenii*, have two flagella: one covered with fine, stiff hairs and a shorter one that is smooth.



Diatoms

A key group of photosynthetic protists, **diatoms** are unicellular algae that have a unique glass-like wall made of silicon dioxide embedded in an organic matrix **(Figure 28.12)**. The wall consists of two parts that overlap like a shoe box and its lid. These walls provide effective protection from the crushing jaws of predators: Live diatoms can withstand pressures as great as 1.4 million kg/m^2, equal to the pressure under each leg of a table supporting an elephant!

With an estimated 100,000 living species, diatoms are a highly diverse group of protists (see Figure 28.5). They are among the most abundant photosynthetic organisms both in the ocean and in lakes: One bucket of water scooped from the surface of the sea may contain millions of these microscopic algae. The abundance of diatoms in the past is also evident in the fossil record, where massive accumulations of fossilized diatom walls are major constituents of sediments known as *diatomaceous earth*. These sediments are mined for their quality as a filtering medium and for many other uses.

▶ Figure 28.12 The diatom *Triceratium morlandii*. (colorized SEM)



Diatoms are so widespread and abundant that their photosynthetic activity affects global carbon dioxide (CO_2) levels. Diatoms have this effect in part because of events that occur during episodes of rapid population growth, or *blooms*, when ample nutrients are available. Typically, diatoms are eaten by a variety of protists and invertebrates, but during a bloom, many escape this fate. When these uneaten diatoms die, their bodies sink to the ocean floor. It takes decades, or even centuries, for dead diatoms that sink to the ocean floor to be broken down by bacteria and other decomposers. As a result, the carbon in their bodies remains there for some time, rather than being released immediately as CO_2 as the decomposers respire. The overall effect of these events is that CO_2 absorbed by diatoms during photosynthesis is transported, or "pumped," to the ocean floor.

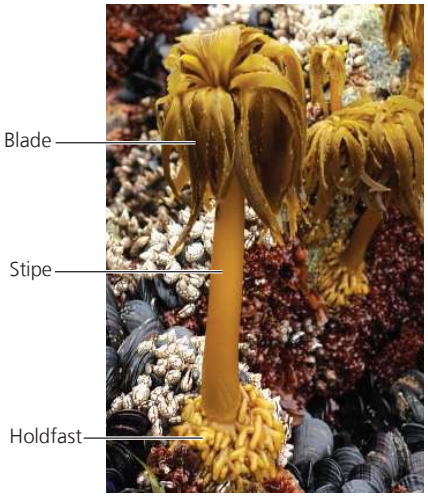
With an eye toward reducing global warming by lowering atmospheric CO_2 levels, some scientists advocate promoting diatom blooms by fertilizing the ocean with essential nutrients such as iron. In one recent study, researchers found that CO_2 was indeed pumped to the ocean floor after iron was added to a small region of the ocean. Further tests are planned to examine whether iron fertilization has undesirable side effects (such as oxygen depletion or the production of nitrous oxide, a more potent greenhouse gas than CO_2).

Brown Algae

The largest and most complex algae are **brown algae**. All are multicellular, and most are marine. Brown algae are especially common along temperate coasts that have cold-water currents. They owe their characteristic brown or olive color to the carotenoids in their plastids.

Many of the species commonly called "seaweeds" are brown algae. Some brown algal seaweeds have specialized structures that resemble organs in plants, such as a rootlike **holdfast**, which anchors the alga, and a stemlike **stipe**, which supports the leaflike **blades (Figure 28.13)**. Unlike plants, however, brown algae lack true tissues and organs. Moreover, morphological and DNA data show that these similarities evolved

▼ Figure 28.13 Seaweeds: adapted to life at the ocean's margins. The sea palm (*Postelsia*) lives on rocks along the coast of the northwestern United States and western Canada. The body of this brown alga is well adapted to maintaining a firm foothold despite the crashing surf.



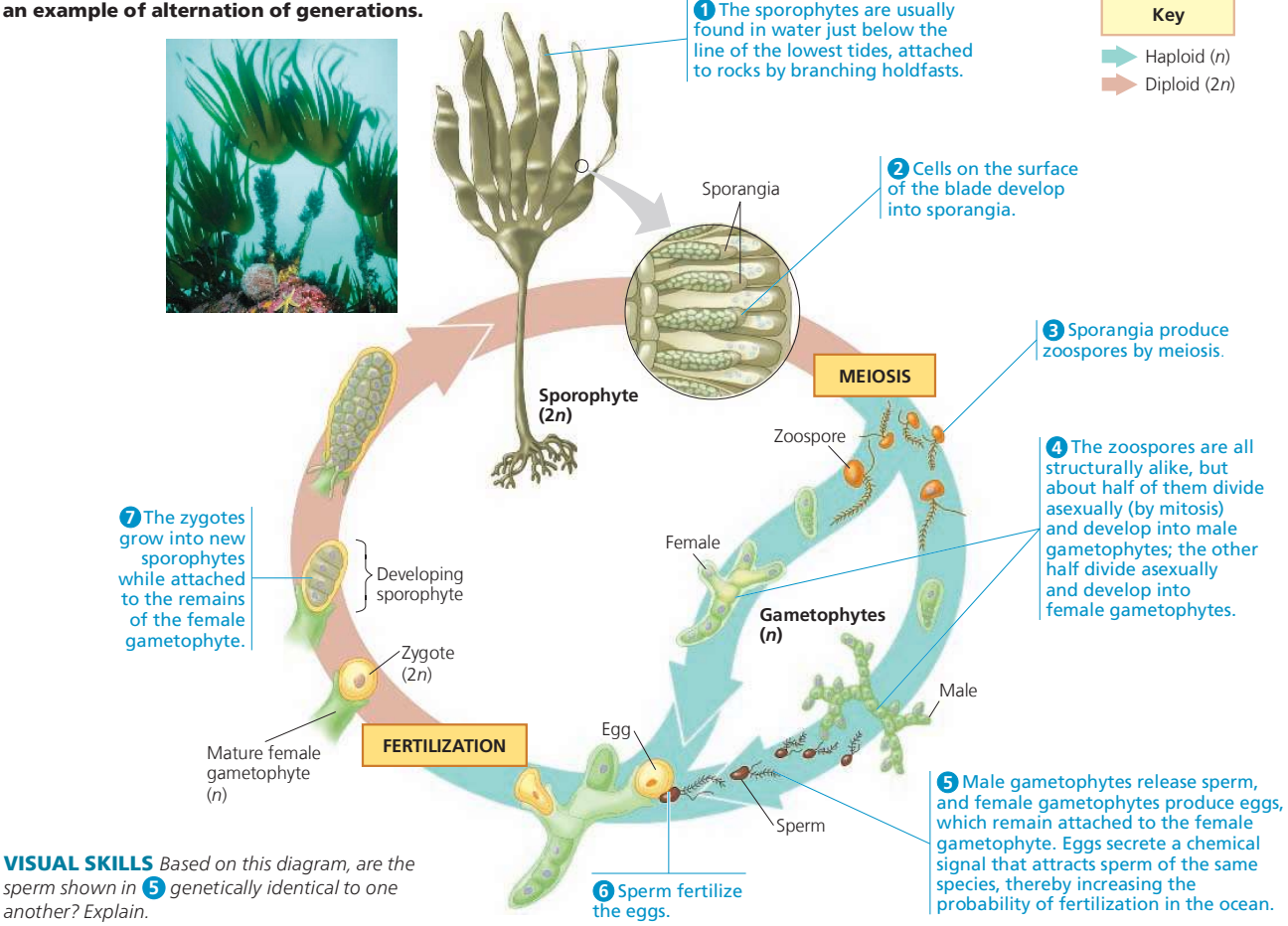
independently in the algal and plant lineages and are thus analogous, not homologous. In addition, while plants have adaptations (such as rigid stems) that provide support against gravity, brown algae have adaptations that enable their main photosynthetic surfaces (the leaflike blades) to be near the water surface. Some brown algae accomplish this task with gas-filled, bubble-shaped floats. Giant brown algae known as kelps that live in deep waters have such floats in their blades, which are attached to stipes that can rise as much as 60 m from the seafloor—more than half the length of a football field.

Brown algae are important commodities for humans. Some species are eaten, such as *Laminaria* (Japanese "kombu"), which is used in soups. In addition, the cell walls of brown algae contain a gel-forming substance, called algin, which is used to thicken many processed foods, including pudding and salad dressing.

Alternation of Generations

A variety of life cycles have evolved among the multicellular algae. The most complex life cycles include an **alternation of generations**, the alternation of multicellular haploid and diploid forms, as shown in **Figure 28.14** for the brown alga

▼ Figure 28.14 The life cycle of the brown alga *Laminaria*: an example of alternation of generations.



VISUAL SKILLS *Based on this diagram, are the sperm shown in 5 genetically identical to one another? Explain.*

Laminaria. Although haploid and diploid conditions alternate in *all* sexual life cycles—human gametes, for example, are haploid—the term *alternation of generations* applies only to life cycles in which both haploid and diploid stages are multicellular. As you will read in Concept 29.1, alternation of generations also evolved in plants.

As detailed in Figure 28.14, the diploid individual in this complex algal life cycle is called the *sporophyte* because it produces spores. The spores are haploid and move by means of flagella; they are called zoospores. The zoospores divide by mitosis and develop into haploid, multicellular male and female *gametophytes*, which produce gametes. The union of two gametes (fertilization) results in a diploid zygote, which matures and gives rise to a new multicellular sporophyte.

In *Laminaria*, the two generations are **heteromorphic**, meaning that the sporophytes and gametophytes are structurally different. Other algal life cycles have an alternation of **isomorphic** generations, in which the sporophytes and gametophytes look similar to each other, although they differ in chromosome number.

Oomycetes (Water Molds and Their Relatives)

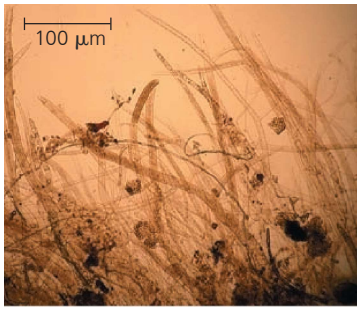
Oomycetes include the water molds, the white rusts, and the downy mildews. Based on their morphology, these organisms were previously classified as fungi (in fact, oomycete means "egg fungus"). For example, many oomycetes have multinucleate filaments (hyphae) that resemble fungal hyphae **(Figure 28.15a)**. However, there are key differences between oomycetes and fungi. Among them, oomycetes typically have cell walls made of cellulose, whereas the walls of fungi consist mainly of another polysaccharide, chitin. Data from molecular systematics have confirmed that oomycetes are not closely related to fungi. In both oomycetes and fungi, the high surface-to-volume ratio of filamentous structures enhances the uptake of nutrients from the environment.

Although oomycetes descended from plastid-bearing ancestors, they no longer have plastids and do not perform photosynthesis. Instead, they typically acquire nutrients as decomposers or parasites. Most water molds are decomposers that grow as cottony masses on dead algae and animals, mainly in freshwater habitats **(Figure 28.15b)**. White rusts and downy mildews generally live on land as plant parasites.

The ecological impact of oomycetes can be significant. For example, the oomycete *Phytophthora infestans* causes potato late blight, which turns the stalks and stems of potato (and tomato) plants into black slime. Late blight contributed to the devastating Irish famine of the 19th century, in which a million people died and at least that many were forced to leave Ireland. The disease remains a major problem today, causing crop losses as high as 70% in some regions. Globally, about $1 billion is spent each year on pesticides to control the parasite.

▼ Figure 28.15 Oomycetes.

(a) Closeup of oomycete hyphae (LM)



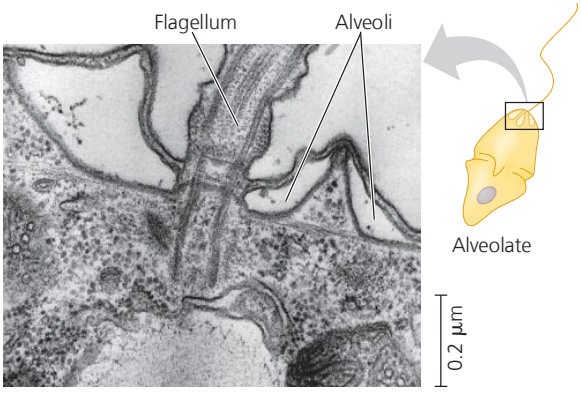
(b) Water mold hyphae growing on a goldfish



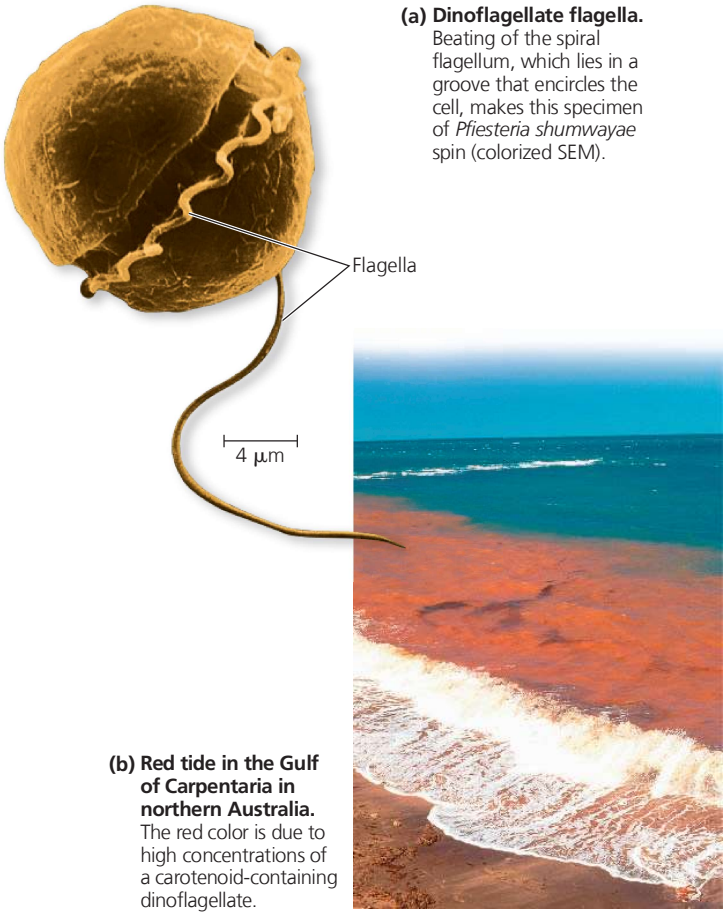
Alveolates

Members of the next subgroup of SAR, the **alveolates**, have membrane-enclosed sacs (alveoli) just under the plasma membrane **(Figure 28.16)**. Alveolates are abundant in many habitats and include a wide range of photosynthetic and heterotrophic protists. We'll discuss three alveolate clades here: a group of flagellates (the dinoflagellates), a group of parasites (the apicomplexans), and a group of protists that move using cilia (the ciliates).

▼ Figure 28.16 Alveoli. These sacs under the plasma membrane are a characteristic that distinguishes alveolates from other eukaryotes (TEM).



▼ **Figure 28.17 Dinoflagellates.**



(a) Dinoflagellate flagella. Beating of the spiral flagellum, which lies in a groove that encircles the cell, makes this specimen of *Pfiesteria shumwayae* spin (colorized SEM).

(b) Red tide in the Gulf of Carpentaria in northern Australia. The red color is due to high concentrations of a carotenoid-containing dinoflagellate.

Mastering Biology Video: Dinoflagellate

Dinoflagellates

The cells of many **dinoflagellates** are reinforced by cellulose plates. Grooves in this "armor" house two flagella, one of which causes dinoflagellates (from the Greek *dinos*, whirling) to spin as they move through the waters of their marine and freshwater communities **(Figure 28.17a)**.

Although their ancestors may have originated by secondary endosymbiosis (see Figure 28.3), roughly half of all dinoflagellate species are now purely heterotrophic. Others are important species of *phytoplankton* (photosynthetic plankton, which include photosynthetic bacteria as well as algae); many photosynthetic dinoflagellates are mixotrophic.

Periods of explosive population growth (blooms) in dinoflagellates sometimes cause a phenomenon called "red tide" **(Figure 28.17b)**. The blooms make coastal waters appear brownish red or pink because of the presence of carotenoids, the most common pigments in dinoflagellate plastids. When blooms occur, toxins produced by certain dinoflagellates have caused massive kills of invertebrates and fishes. Humans who eat molluscs that have accumulated the toxins are affected as well, sometimes fatally. A 2017 study found that ocean warming (caused by ongoing climate change) has facilitated more frequent blooms of toxic dinoflagellates, making them a growing threat to human health.

Apicomplexans

Nearly all **apicomplexans** are parasites of animals—and virtually all animal species examined so far are attacked by these parasites. The parasites spread through their host as tiny infectious cells called *sporozoites*. Apicomplexans are so named because one end (the *apex*) of the sporozoite cell contains a *complex* of organelles specialized for penetrating host cells and tissues. Although apicomplexans are not photosynthetic, recent data show that they retain a modified plastid (apicoplast), most likely of red algal origin.

Most apicomplexans have intricate life cycles with both sexual and asexual stages. Those life cycles often require two or more host species for completion. For example, *Plasmodium*, the parasite that causes malaria, lives in both mosquitoes and humans **(Figure 28.18)**.

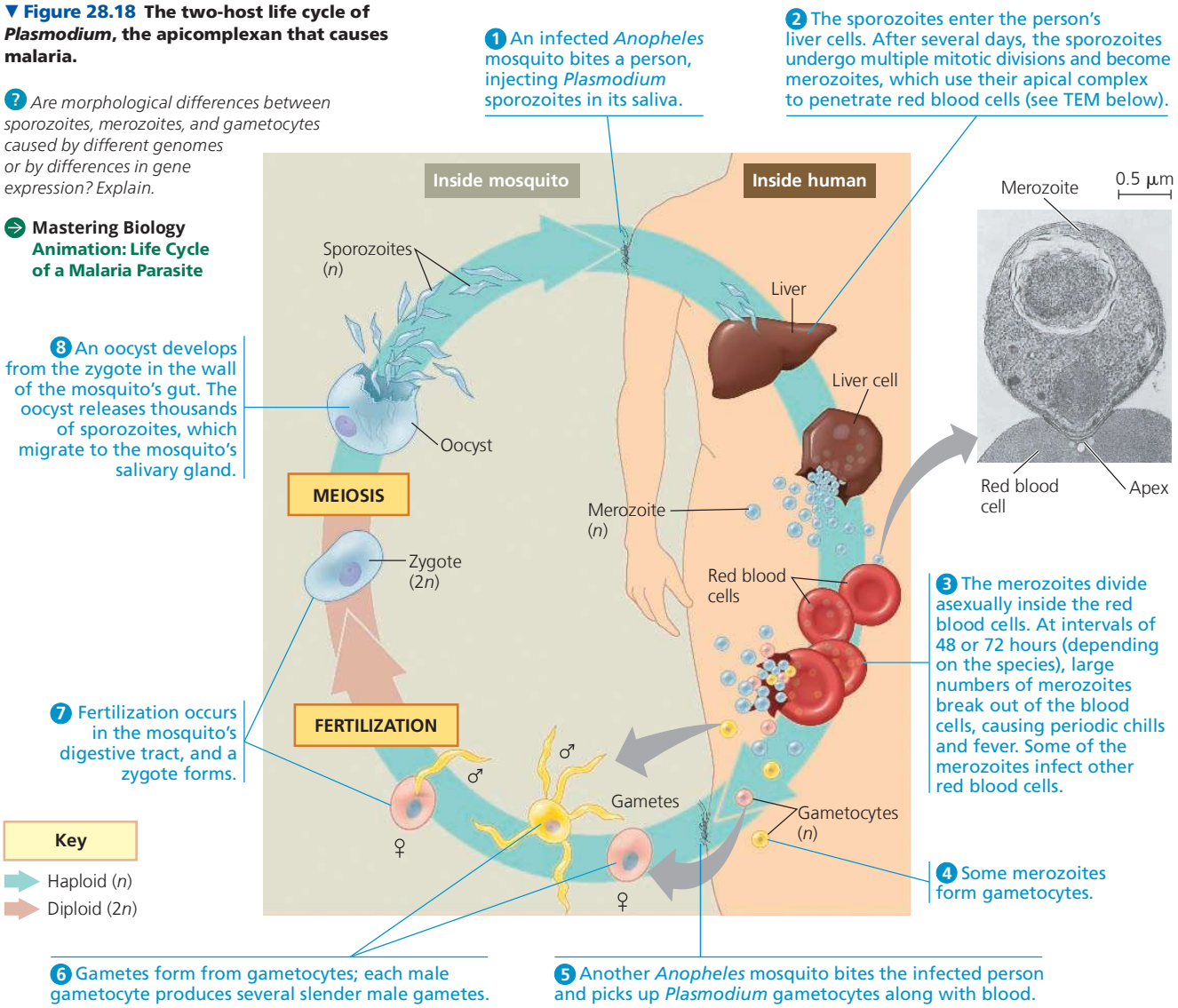
Historically, malaria has rivaled tuberculosis as the leading cause of human death by infectious disease. The incidence of malaria was diminished in the 1960s by insecticides that reduced carrier populations of *Anopheles* mosquitoes and by drugs that killed *Plasmodium* in humans. But the emergence of resistant varieties of both *Anopheles* and *Plasmodium* has led to a resurgence of malaria. About 220 million people in the tropics are currently infected, and 450,000 die each year. In regions where malaria is common, the lethal effects of this disease have resulted in the evolution of high frequencies of the sickle-cell allele; for an explanation of this connection, see Figure 23.18.

The search for malarial vaccines has been hampered by the fact that *Plasmodium* lives mainly inside cells, hidden from the host's immune system. And, like trypanosomes, *Plasmodium* continually changes its surface proteins. Even so, significant progress was made when European regulators recently approved the world's first licensed malarial vaccine. In 2019, routine use of this vaccine began in selected regions of Africa. However, this vaccine, which targets a protein on the surface of sporozoites, provides only partial protection against malaria. As a result, researchers continue to study other potential vaccine targets, including the apicoplast. This approach may be effective because the apicoplast is a modified plastid; as such, it descended from a cyanobacterium and hence has different metabolic pathways from those in human patients.

▼ Figure 28.18 The two-host life cycle of *Plasmodium*, the apicomplexan that causes malaria.

? *Are morphological differences between sporozoites, merozoites, and gametocytes caused by different genomes or by differences in gene expression? Explain.*

Mastering Biology Animation: Life Cycle of a Malaria Parasite



Ciliates

The **ciliates** are a large and varied group of protists named for their use of cilia to move and feed **(Figure 28.19a)**. Most ciliates are predators, typically of bacteria or of other protists. Their cilia may completely cover the cell surface or may be clustered in a few rows or tufts. In certain species, rows of tightly packed cilia function collectively in locomotion. Other ciliates scurry about on leg-like structures constructed from many cilia bonded together.

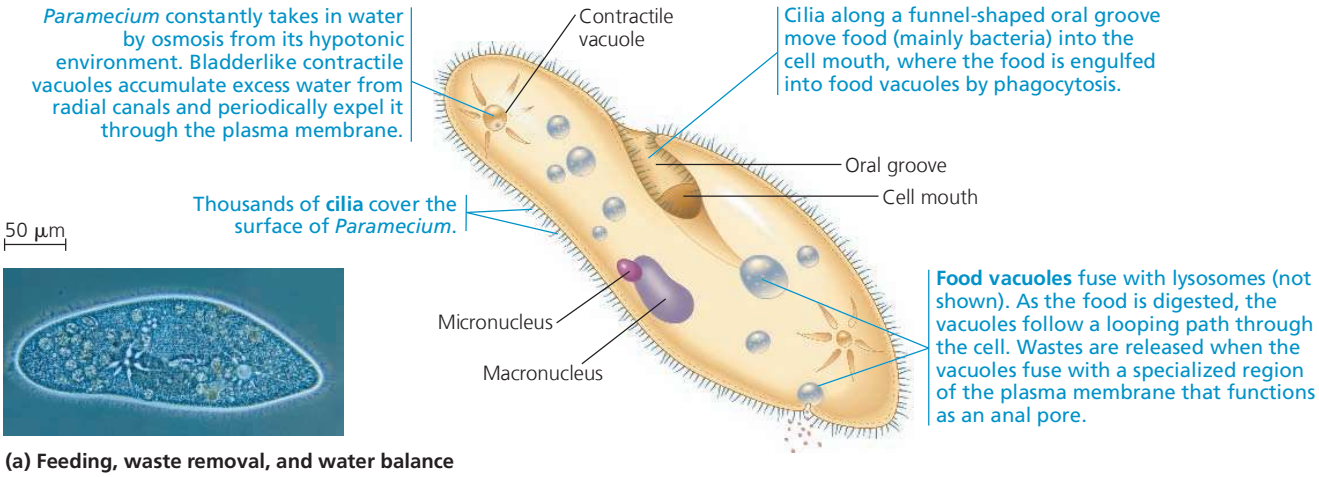
A distinctive feature of ciliates is the presence of two types of nuclei: tiny micronuclei and large macronuclei. A cell has one or more nuclei of each type. Genetic variation results from **conjugation**, a sexual process in which two individuals exchange haploid micronuclei but do not reproduce **(Figure 28.19b)**. Ciliates generally reproduce asexually by binary fission, during which the existing macronucleus disintegrates and a new one is formed from the cell's micronuclei. Each macronucleus typically contains multiple copies of the ciliate's genome. Genes in the macronucleus control the everyday functions of the cell, such as feeding, waste removal, and maintaining water balance.

Mastering Biology Video: Ciliate Movement in *Stentor*

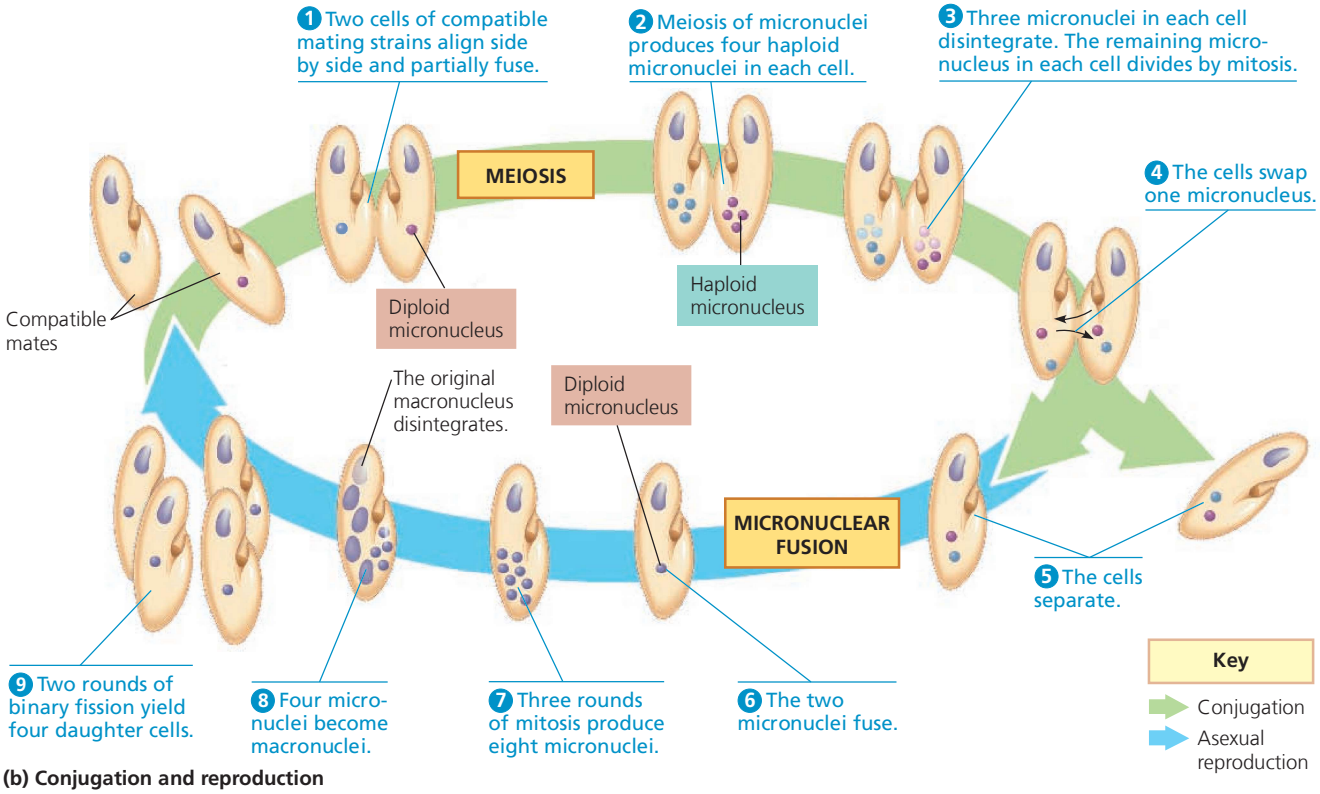
Rhizarians

Our next subgroup of SAR is the **rhizarians**. Many species in this group are **amoebas**, protists that move and feed by

▼ Figure 28.19 Structure and function in the ciliate *Paramecium caudatum*.



(a) Feeding, waste removal, and water balance



(b) Conjugation and reproduction

MAKE CONNECTIONS *The events shown in steps 4 through 6 of this diagram have a similar overall effect to what event in the human life cycle (see Figure 13.5)? Explain.*

Mastering Biology Video: *Paramecium*

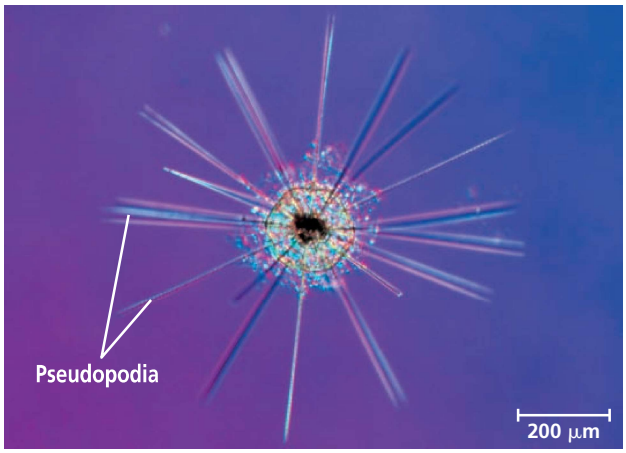
means of **pseudopodia**, extensions that may bulge from almost anywhere on the cell surface. An amoeba moves by extending a pseudopodium and anchoring its tip; more cytoplasm then streams into the pseudopodium. Amoebas do not constitute a monophyletic group; instead, they are dispersed across many distantly related eukaryotic taxa. Most amoebas that are rhizarians differ morphologically from other amoebas by having threadlike pseudopodia. Rhizarians also include flagellated (non-amoeboid) protists that feed using threadlike pseudopodia.

We'll examine three groups of rhizarians here: radiolarians, forams, and cercozoans.

Radiolarians

The protists called **radiolarians** have delicate, intricately symmetrical internal skeletons that are generally made of silica. The pseudopodia of these mostly marine protists radiate from the central body **(Figure 28.20)** and are reinforced by bundles of microtubules. The microtubules are covered by a thin layer of cytoplasm, which engulfs smaller microorganisms that become attached to the pseudopodia. Cytoplasmic streaming then carries the captured prey into the main part of the cell. After radiolarians die, their skeletons settle to the seafloor, where they have accumulated as an ooze that is hundreds of meters thick in some locations.

▼ Figure 28.20 A radiolarian. Numerous threadlike pseudopodia radiate from the central body of this radiolarian (LM).



Forams

The protists called **foraminiferans** (from the Latin *foramen*, little hole, and *ferre*, to bear), or **forams**, are named for their porous shells, called **tests** (see Figure 28.5). Foram tests consist of a single piece of organic material that typically is hardened with calcium carbonate. The pseudopodia that extend through the pores function in swimming, test formation, and feeding. Many forams also derive nourishment from the photosynthesis of symbiotic algae that live within the tests.

Forams are found in both the ocean and fresh water. Most species live in sand or attach themselves to rocks or algae, but some live as plankton. The largest forams, though single-celled, have tests several centimeters in diameter.

Ninety percent of all identified species of forams are known from fossils. Along with the calcium-containing remains of other protists, the fossilized tests of forams are part of marine sediments, including sedimentary rocks that are now land formations. Foram fossils are excellent markers for correlating the ages of sedimentary rocks in different parts of the world. Researchers are also studying these fossils to obtain information about climate change and its effects on the oceans and their life **(Figure 28.21)**.

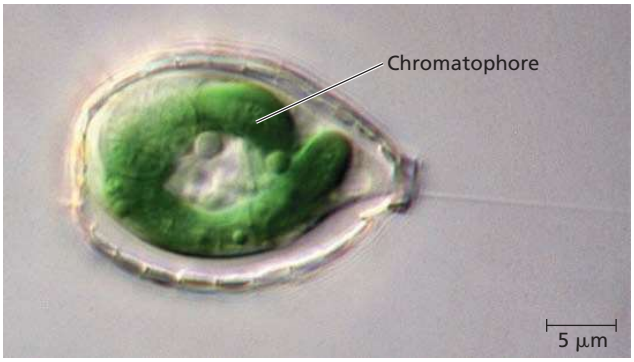
▼ Figure 28.21 Fossil forams. By measuring the magnesium content in fossilized forams like these, researchers seek to learn how ocean temperatures have changed over time. Forams take up more magnesium in warmer water than in colder water.



Cercozoans

First identified in molecular phylogenies, the **cercozoans** are a large group of amoeboid and flagellated protists that feed using threadlike pseudopodia. Cercozoan protists are common inhabitants of marine, freshwater, and soil ecosystems.

▼ Figure 28.22 A second case of primary endosymbiosis? The cercozoan *Paulinella* conducts photosynthesis in a unique sausage-shaped structure called a chromatophore (LM). Chromatophore membranes include a peptidoglycan layer, indicating that they are derived from a bacterium. DNA evidence shows that chromatophores are derived from a different cyanobacterium than that from which plastids are derived.



Most cercozoans are heterotrophs. Many are parasites of plants, animals, or other protists; many others are predators. The predators include the most important consumers of bacteria in aquatic and soil ecosystems, along with species that eat other protists, fungi, and even small animals. One small group of cercozoans, the chlorarachniophytes (mentioned earlier in the discussion of secondary endosymbiosis), are mixotrophic: These organisms ingest smaller protists and bacteria as well as perform photosynthesis. At least one other cercozoan, *Paulinella chromatophora*, is an autotroph, deriving its energy from light and its carbon from CO_2. *Paulinella* **(Figure 28.22)** appears to represent an intriguing additional evolutionary example of a eukaryotic lineage that obtained its photosynthetic apparatus directly from a cyanobacterium.

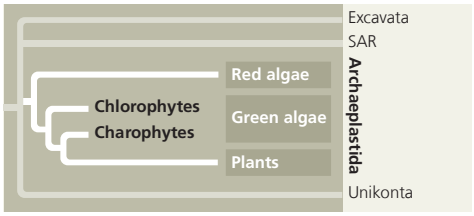
CONCEPT CHECK 28.3

1. Explain why forams have such a well-preserved fossil record.
2. **WHAT IF?** Would you expect the plastid DNA of photosynthetic dinoflagellates and diatoms to be more similar to the nuclear DNA of plants (domain Eukarya) or to the chromosomal DNA of cyanobacteria (domain Bacteria)? Explain.
3. **MAKE CONNECTIONS** Which of the three life cycles in Figure 13.6 exhibits alternation of generations? How does it differ from the other two?
4. **MAKE CONNECTIONS** Review Figures 9.2 and 10.5, and then summarize how CO_2 and O_2 are both used and produced by chlorarachniophytes and other aerobic algae.

For suggested answers, see Appendix A.

CONCEPT 28.4

Red algae and green algae are the closest relatives of plants



As described earlier, morphological and molecular evidence indicates that plastids arose when a heterotrophic protist acquired a cyanobacterial endosymbiont. Later, photosynthetic descendants of this ancient protist evolved into red algae and green algae (see Figure 28.3), and the lineage that produced green algae then gave rise to plants. Together, red algae, green algae, and plants make up our third eukaryotic supergroup, which is called **Archaeplastida**. Archaeplastida is a monophyletic group that descended from the ancient protist that engulfed a cyanobacterium. We will examine plants in Chapters 29 and 30; here we will look at the diversity of their closest algal relatives, red algae and green algae.

Red Algae

Many of the 6,000 known species of **red algae** (rhodophytes, from the Greek *rhodos*, red) are reddish, owing to the photosynthetic pigment phycoerythrin, which masks the green of chlorophyll **(Figure 28.23)**. However, other species (those adapted to shallow water) have less phycoerythrin. As a result, red algal species may be greenish red in very shallow water, bright red at moderate depths, and almost black in deep water. Some species lack pigmentation altogether and live as heteroptrophic parasites on other red algae.

Figure 28.23 Red algae.

Bonnemaisonia hamifera. This red alga has a filamentous form.



8 mm



Dulse (*Palmaria palmata*). This edible species has a "leafy" form.

Nori. The red alga *Porphyra* is the source of a traditional Japanese food.



The seaweed is grown on nets in shallow coastal waters.



Paper-thin, glossy sheets of dried nori make a mineral-rich wrap for rice, seafood, and vegetables in sushi.

Red algae are abundant in the warm coastal waters of tropical oceans. Some of their photosynthetic pigments, including phycoerythrin, allow them to absorb blue and green light, which penetrate relatively far into the water. A species of red alga has been discovered near the Bahamas at a depth of more than 260 m. There are also a small number of freshwater and terrestrial species.

Most red algae are multicellular. Although none are as big as the giant brown kelps, the largest multicellular red algae are included in the informal designation "seaweeds." You may have eaten one of these multicellular red algae, *Porphyra* (Japanese "nori"), as crispy sheets or as a wrap for sushi (see Figure 28.23). Red algae reproduce sexually and have diverse life cycles in which alternation of generations is common. However, unlike other algae, red algae do not have flagellated gametes, so they depend on water currents to bring gametes together for fertilization.

Green Algae

The grass-green chloroplasts of **green algae** have a structure and pigment composition much like the chloroplasts of plants. Molecular systematics and cellular morphology leave little doubt that green algae and plants are closely related. In fact, some systematists now advocate including green algae in an expanded "plant" kingdom, Viridiplantae (from the Latin *viridis*, green). Phylogenetically, this change makes sense, since otherwise the green algae are a paraphyletic group.

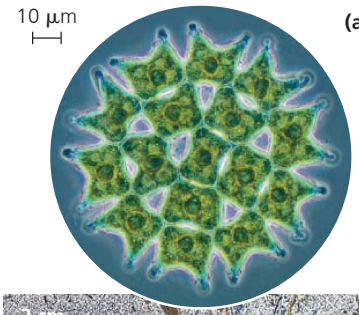
Green algae can be divided into two main groups, the charophytes and the chlorophytes. The charophytes include the algae most closely related to plants, and we will discuss them along with plants in Chapter 29.

The second group, the chlorophytes (from the Greek *chloros*, green), includes more than 7,000 species. Most live in fresh water, but there are also many marine and some terrestrial species. The simplest chlorophytes are unicellular organisms such as *Chlamydomonas*, which resemble gametes of more complex chlorophytes. Various species of unicellular chlorophytes live independently in aquatic habitats as phytoplankton or inhabit damp soil. Some live symbiotically within other eukaryotes, contributing part of their photosynthetic output to the food supply of their hosts. Still other chlorophytes live in environments exposed to intense visible and ultraviolet radiation; these species are protected by radiation-blocking compounds in their cytoplasm, cell wall, or zygote coat.

Larger size and greater complexity evolved in green algae by three different mechanisms:

1. The formation of colonies of individual cells, as seen in *Pediastrum* **(Figure 28.24a)** and other species that contribute to the stringy masses known as pond scum.

▼ Figure 28.24 Examples of large chlorophytes.



(a) *Pediastrum*, a pond alga. Chlorophytes in this genus form daughter colonies with the same number and arrangement of cells as the parent colony.



(b) *Ulva*, or sea lettuce. This multicellular, edible chlorophyte has differentiated structures, such as its leaflike blades and a rootlike holdfast that anchors the alga.



(c) *Caulerpa*, an intertidal chlorophyte. The branched filaments lack cross-walls and thus are multinucleate. In effect, the body of this alga is one huge "supercell."

2. The formation of true multicellular bodies by cell division and differentiation, as in *Volvox* (see Figure 28.5) and *Ulva* **(Figure 28.24b)**.
3. The repeated division of nuclei with no cytoplasmic division, as in *Caulerpa* **(Figure 28.24c)**.

Most chlorophytes have complex life cycles, with both sexual and asexual reproductive stages. Nearly all species of chlorophytes reproduce sexually by means of biflagellated gametes that have cup-shaped chloroplasts **(Figure 28.25)**. Alternation of generations has evolved in some chlorophytes, including *Ulva*.

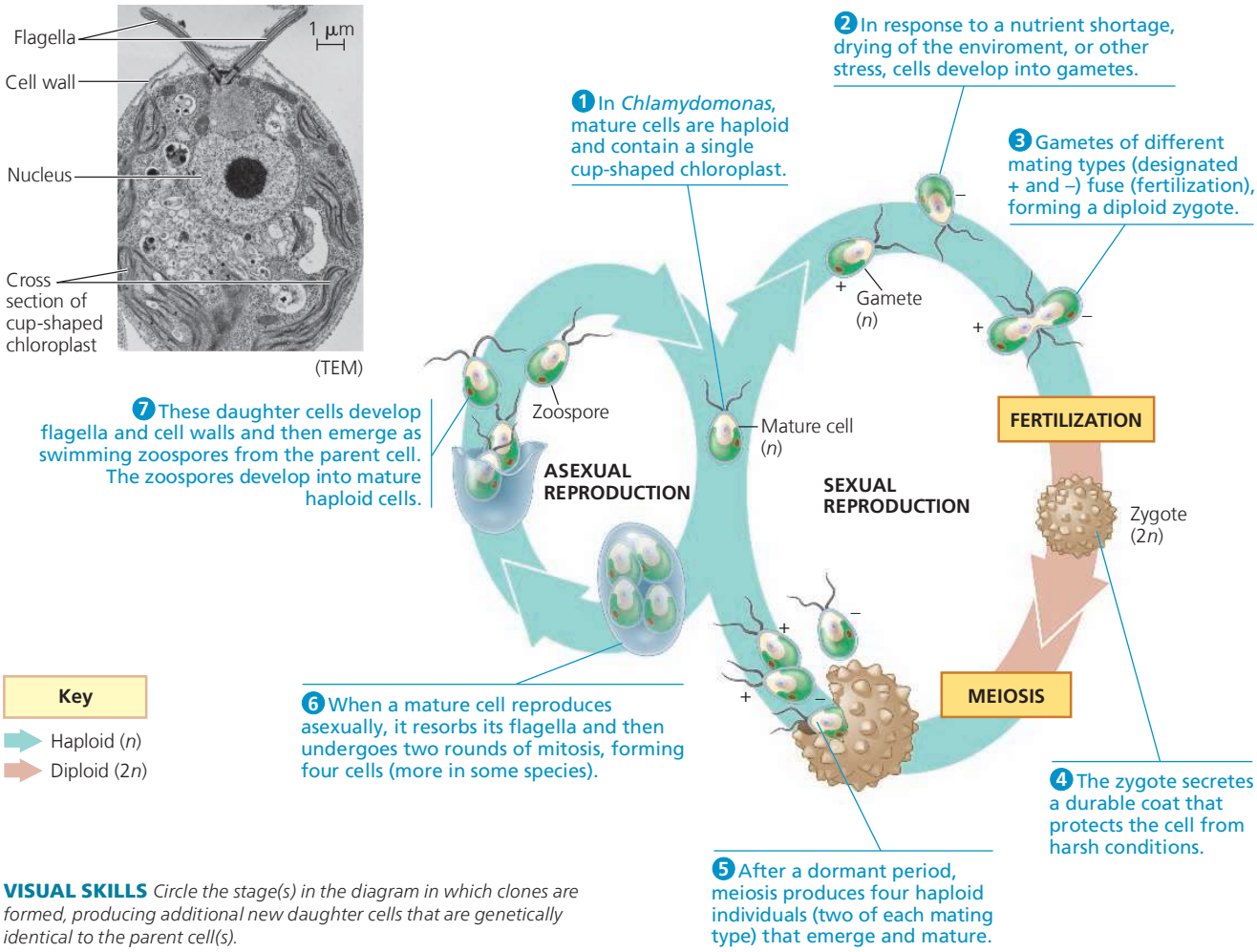
Mastering Biology **Animation: Alternation of Generations in a Protist**

CONCEPT CHECK 28.4

1. Contrast red algae and brown algae.
2. Why is it accurate to say that *Ulva* is truly multicellular but *Caulerpa* is not?
3. **WHAT IF?** Suggest a possible reason why species in the green algal lineage may have been more likely to colonize land than species in the red algal lineage.

For suggested answers, see Appendix A.

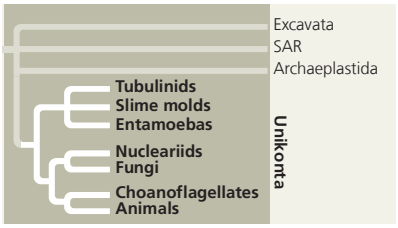
▼ Figure 28.25 The life cycle of *Chlamydomonas*, a unicellular chlorophyte.



VISUAL SKILLS *Circle the stage(s) in the diagram in which clones are formed, producing additional new daughter cells that are genetically identical to the parent cell(s).*

CONCEPT 28.5

Unikonts include protists that are closely related to fungi and animals



Unikonta (also called Amorphea) is an extremely diverse supergroup of eukaryotes that includes animals, fungi, and some protists. There are two major clades of unikonts, the amoebozoans (tubulinids and close protist relatives) and the opisthokonts (animals, fungi, and closely related protist groups). Each of these two major clades is strongly supported by molecular systematics. Support for the close relationship between amoebozoans and opisthokonts is provided by comparisons of myosin proteins and by some (but not all) studies based on multiple genes or whole genomes.

An ongoing debate involving the unikonts concerns the root of the eukaryotic tree. Recall that the root of a phylogenetic tree anchors the tree in time: Branch points close to the root are the oldest. At present, the root of the eukaryotic tree is uncertain; hence, we do not know which supergroup of eukaryotes was the first to diverge from all other eukaryotes. If the root of the eukaryotic tree were known, it would help scientists infer characteristics of the common ancestor of all eukaryotes.

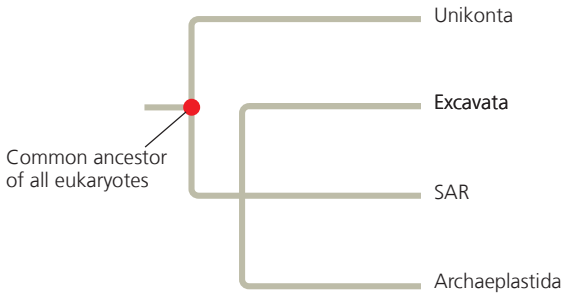
In trying to determine the root of the eukaryotic tree, researchers have based their phylogenies on different sets of genes, with conflicting results. Researchers have also tried a different approach, based on tracing the evolutionary history of genes that were transferred to eukaryotes from bacterial

▼ Figure 28.26 Inquiry

What is the root of the eukaryotic tree?

Experiment Responding to the difficulty in determining the root of the eukaryotic phylogenetic tree, Romain Derelle and colleagues used a new approach. They studied 39 nuclear genes that eukaryotes acquired by horizontal gene transfer from a single bacterial source: the alpha proteobacterium endosymbiont that gave rise to the mitochondrion. These 39 genes were known to be orthologous (see Figure 26.18). As a result, differences among these genes reflect the history of speciation events that have occurred since the eukaryotes began to diverge from their last common ancestor—making these genes well suited for inferring the root of the eukaryotic tree. Derelle and colleagues obtained the sequences of these genes for 67 species of eukaryotes representing a wide range of eukaryotic taxa. Those sequences were then used to infer evolutionary relationships among the four eukaryotic supergroups shown in Figure 28.5.

Results



Conclusion The results show that Excavata, SAR, and Archaeplastida form a clade, which supports the hypothesis that the root of the tree is located between the unikonts and all other eukaryotes.

Data from R. Derelle et al., Bacterial proteins pinpoint a single eukaryotic root, *Proceedings of the National Academy of Sciences USA* 112:E693–699 (2015).

WHAT IF? *Other recent evidence indicates that the root of the eukaryotic tree may lie between a clade that includes unikonts and excavates and all other eukaryotes. Draw the tree suggested by this result.*

donors **(Figure 28.26)**. Results from this approach indicate that Excavata, SAR, and Archaeplastida share a more recent common ancestor than any of them does with Unikonta. This suggests that the root of the tree is located between the unikonts and all other eukaryotes, which implies that the unikonts were the first eukaryotic supergroup to diverge from all other eukaryotes. This idea remains controversial and will require more supporting evidence to be widely accepted.

Amoebozoans

The **amoebozoan** clade includes many species of amoebas that have lobe- or tube-shaped pseudopodia rather than the threadlike pseudopodia found in rhizarians. Amoebozoans include tubulinids, slime molds, and entamoebas.

Tubulinids

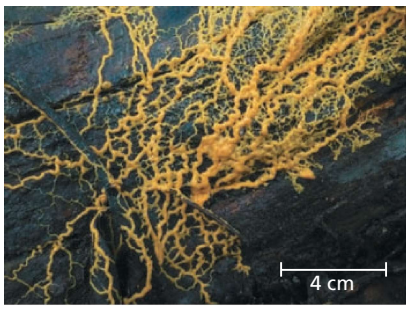
Tubulinids constitute a large and varied group of amoebozoans that have lobe- or tube-shaped pseudopodia. These unicellular protists are ubiquitous in soil as well as freshwater and marine environments. Most are heterotrophs that actively seek and consume bacteria and other protists; one such tubulinid species, *Amoeba proteus*, is shown in Figure 28.5. Some tubulinids also feed on detritus (nonliving organic matter).

Slime Molds

Slime molds, or mycetozoans (from the Latin, meaning "fungus animals"), once were thought to be fungi because, like fungi, they produce fruiting bodies that aid in spore dispersal. However, DNA sequence analyses indicate that the resemblance between slime molds and fungi is a case of evolutionary convergence. Slime molds have diverged into two main branches, plasmodial slime molds and cellular slime molds. We'll compare their characteristics and life cycles.

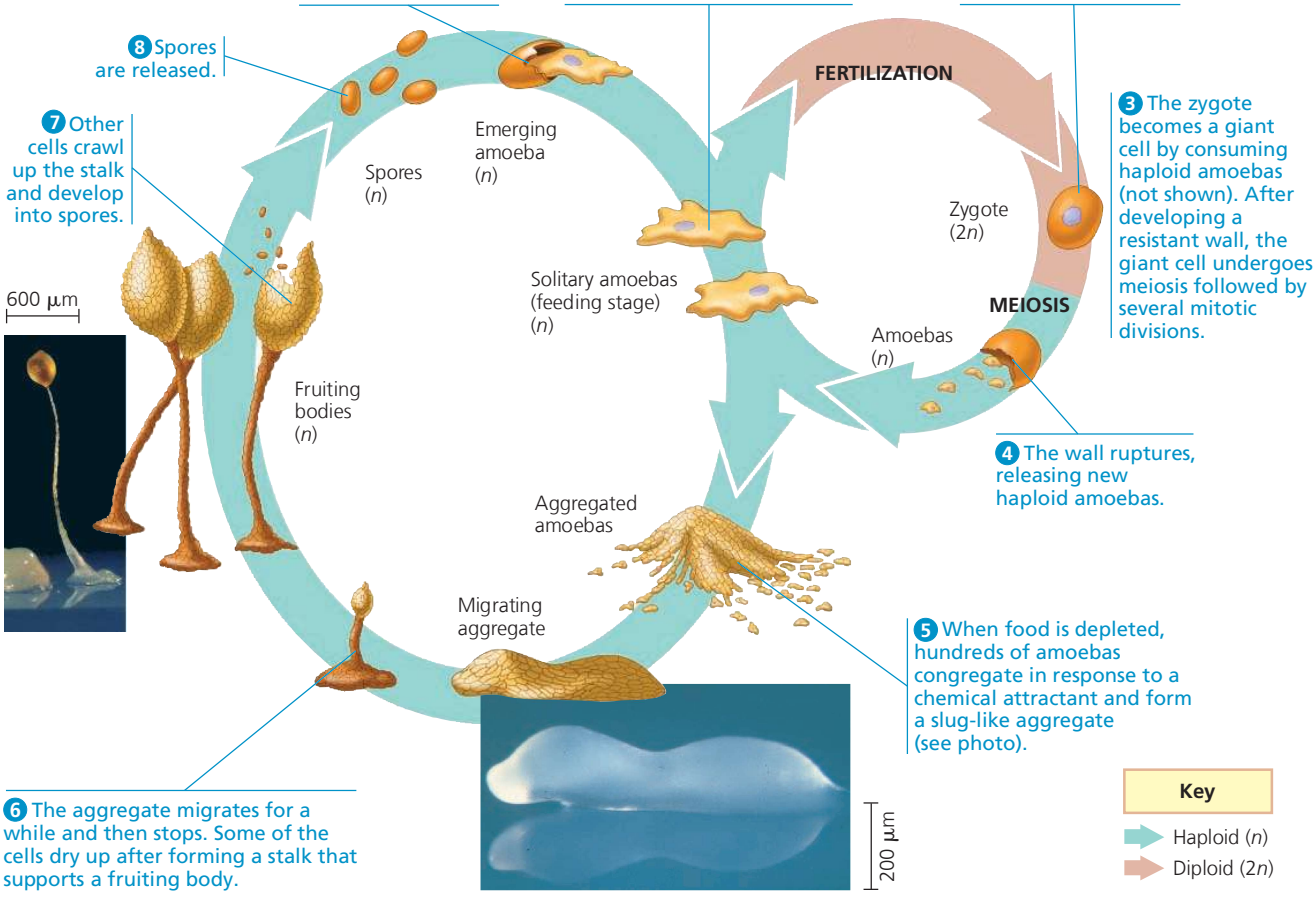
Plasmodial Slime Molds Many plasmodial slime molds are brightly colored, often yellow or orange **(Figure 28.27)**. As they grow, they form a mass called a plasmodium, which can be many centimeters in diameter. (Don't confuse a slime mold's plasmodium with the genus *Plasmodium*, which includes the parasitic apicomplexan that causes malaria.) Despite its size, the plasmodium is not multicellular; it is a single mass of cytoplasm that is undivided by plasma membranes and that contains many nuclei. This "supercell" is the product of mitotic nuclear divisions that are not followed by cytokinesis. The plasmodium extends pseudopodia through moist soil, leaf mulch, or rotting logs, engulfing food particles by phagocytosis as it grows. If the habitat begins to dry up or there is no food left, the plasmodium stops growing and differentiates into fruiting bodies that function in sexual reproduction.

▶ Figure 28.27 A mature plasmodium, the feeding stage in the life cycle of a plasmodial slime mold.



Cellular Slime Molds The life cycle of the protists called cellular slime molds can prompt us to question what it means to be an individual organism. The feeding stage of these organisms consists of solitary cells that function individually, but when food is depleted, the cells form a slug-like aggregate that functions as a unit **(Figure 28.28)**. Unlike the feeding stage (plasmodium) of a plasmodial slime mold, these aggregated cells remain separated by their individual plasma membranes. Ultimately, the aggregated cells form an asexual fruiting body.

▼ Figure 28.28 The life cycle of *Dictyostelium*, a cellular slime mold.



VISUAL SKILLS *Suppose cells were removed from the slug-like aggregate shown in the photo. Use the information in the life cycle to infer whether these cells would be haploid or diploid. Explain.*

Dictyostelium discoideum, a cellular slime mold commonly found on forest floors, has become a model organism for studying the evolution of multicellularity. One line of research has focused on the slime mold's fruiting body stage. During this stage, the cells that form the stalk die as they dry out, while the spore cells at the top survive and have the potential to reproduce (see Figure 28.28). Scientists have found that mutations in a single gene can turn individual *Dictyostelium* cells into "cheaters" that never become part of the stalk. Because these mutants gain a strong reproductive advantage over noncheaters, why don't all *Dictyostelium* cells cheat?

Recent discoveries suggest an answer to this question. Cheating cells lack a specific surface protein, and noncheating cells can recognize this difference. Noncheaters preferentially aggregate with other noncheaters, thus depriving cheaters of the chance to exploit them. Such a recognition system may have been important in the evolution of other multicellular eukaryotes, such as animals and plants.

Entamoebas

Whereas most amoebozoans are free-living, those that belong to the genus *Entamoeba* are symbiotic parasites. They infect all classes of vertebrate animals as well as some invertebrates. Humans are host to at least six species of *Entamoeba*, but only one, *E. histolytica*, is known to be pathogenic. *E. histolytica* causes amoebic dysentery and is spread via contaminated drinking water, food, or eating utensils. Responsible for up to 110,000 deaths worldwide every year, the disease is the third-leading cause of death due to eukaryotic parasites, after malaria (see Figure 28.18) and schistosomiasis (see Figure 33.10).

Opisthokonts

Opisthokonts are an extremely diverse group of eukaryotes that includes animals, fungi, and several groups of protists. We will discuss the evolutionary history of fungi and animals in Chapters 31–34. Of the opisthokont protists, we will discuss

the nucleariids in Chapter 31 because they are more closely related to fungi than they are to other protists. Similarly, we will discuss choanoflagellates in Chapter 32, since they are more closely related to animals than they are to other protists. The nucleariids and choanoflagellates illustrate why scientists have abandoned the former kingdom Protista: A monophyletic group that includes these single-celled eukaryotes would also have to include the multicellular animals and fungi that are closely related to them.

CONCEPT CHECK 28.5

1. Contrast the pseudopodia of amoebozoans and forams.
2. In what sense is "fungus animal" a fitting description of a slime mold? In what sense is it not fitting?
3. **MAKE CONNECTIONS** Alpha proteobacteria were used as the outgroup to estimate the tree shown in Figure 28.26. Explain why these bacteria were selected as the outgroup rather than other bacterial or archaeal lineages. (See Figure 26.12 and associated text in Concept 26.3.)

For suggested answers, see Appendix A.

CONCEPT 28.6

Protists play key roles in ecological communities

Most protists are aquatic, and they are found almost anywhere there is water, including moist terrestrial habitats such as damp soil and leaf litter. In oceans, ponds, and lakes, many protists are bottom-dwellers that attach to rocks and other substrates or creep through the sand and silt. As we've seen, other protists are important constituents of plankton. We'll focus here on two key roles that protists play in the varied habitats in which they live: that of symbiont and that of producer.

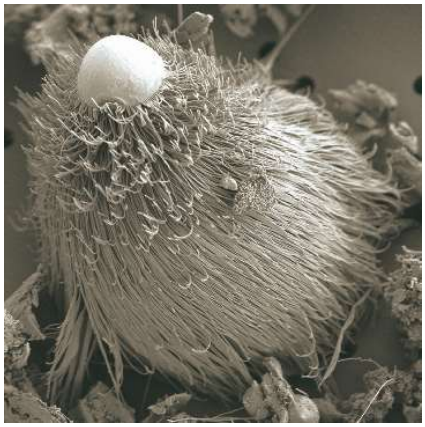
Symbiotic Protists

Many protists form symbiotic associations with other species. For example, photosynthetic dinoflagellates are food-providing symbiotic partners of the animals (coral polyps) that build coral reefs. Coral reefs are highly diverse ecological communities. That diversity ultimately depends on corals—and on the mutualistic protists that nourish them. Corals support reef diversity by providing food to some species and habitat to many others.

Another example is the wood-digesting protists that inhabit the gut of many termite species **(Figure 28.29)**. Unaided, termites cannot digest wood, and they rely on protistan or prokaryotic symbionts to do so. Termites cause over $3.5 billion in damage annually to wooden homes in the United States.

Symbiotic protists also include parasites that have compromised the economies of entire countries. Consider the malaria-causing protist *Plasmodium*: Income levels in countries hard hit by malaria are 33% lower than in similar countries free of the disease. Protists can have devastating effects on other species too. Massive fish kills have been attributed to *Pfiesteria shumwayae* (see Figure 28.17), a dinoflagellate parasite that attaches to its victims and eats their skin. Among species that parasitize plants, the stramenopile *Phytophthora ramorum* (an oomycete) has emerged as a major new forest pathogen. This species causes sudden oak death (SOD), a disease that has killed millions of oaks and other trees in the United States and Great Britain (**Figure 28.30**; also see Concept 54.5).

▶ Figure 28.29 A symbiotic protist. This organism is a hypermastigote, a member of a group of parabasalids that live in the gut of termites and certain cockroaches and enable the hosts to digest wood (SEM).

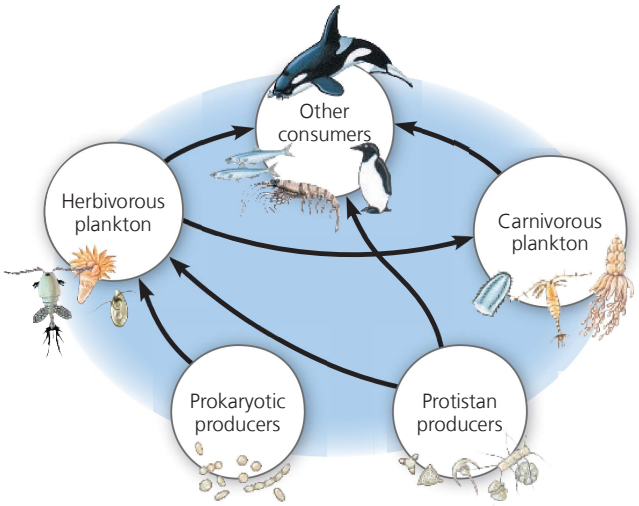


▼ Figure 28.30 Sudden oak death. Many dead oak trees are visible in this Monterey County, California landscape. Infected trees lose their ability to adjust to cycles of wet and dry weather.



Photosynthetic Protists

Many protists are important **producers**, organisms that use energy from light (or in some prokaryotes, inorganic chemicals) to convert CO_2 to organic compounds. Producers form the base of ecological food webs. In aquatic communities, the main producers are photosynthetic protists and prokaryotes **(Figure 28.31)**. All other organisms in the community are **consumers** that depend on producers for food, either directly (by eating them) or indirectly (by eating an organism that ate a producer). Scientists estimate that roughly 30% of the world's photosynthesis is performed by diatoms, dinoflagellates, multicellular algae, and other aquatic protists. Photosynthetic prokaryotes contribute another 20%, and plants are responsible for the remaining 50%.



▲ Figure 28.31 Protists: key producers in aquatic communities. Arrows in this simplified food web lead from food sources to the organisms that eat them.

Because producers form the foundation of food webs, factors that affect producers can dramatically affect their entire community. In aquatic environments, photosynthetic protists are often held in check by low concentrations of nitrogen, phosphorus, or iron. Various human actions can increase the concentrations of these elements in aquatic communities. For example, when fertilizer is applied to a field, some of the fertilizer may be washed by rainfall into a river that drains into a lake or ocean. When people add nutrients to aquatic communities in this or other ways, the abundance of photosynthetic protists can increase spectacularly. Such increases can have major ecological consequences, including the formation of large "dead zones" in marine ecosystems (see Figure 56.23).

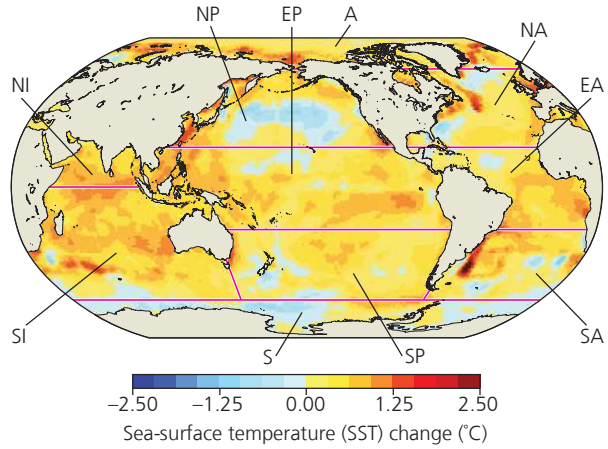
A pressing question is how global warming will affect photosynthetic protists and other producers. As shown in **Figure 28.32**, the growth and biomass of photosynthetic protists and prokaryotes have declined in many ocean regions as sea surface temperatures have increased. By what mechanism do rising sea surface temperatures reduce the growth of marine producers? One hypothesis relates to the rise or upwelling of cold, nutrient-rich waters from below. Many marine producers rely on nutrients brought to the surface in this way. However, rising sea surface temperatures can cause the formation of a layer of light, warm water that acts as a barrier to nutrient upwelling—thus reducing the growth of marine producers. If sustained, the changes shown in Figure 28.32 would likely have far-reaching effects on marine ecosystems, fishery yields, and the global carbon cycle (see Figure 55.14). Global warming can also affect producers on land, but there the base of food webs is occupied not by protists but by plants, which we will discuss in Chapters 29 and 30.

CONCEPT CHECK 28.6

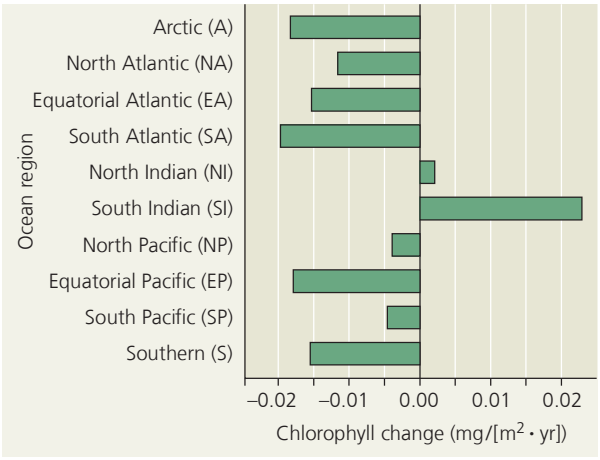
1. Justify the claim that photosynthetic protists are among the biosphere's most important organisms.
2. Describe three symbioses that include protists.
3. **WHAT IF?** High water temperatures and pollution can cause corals to expel their dinoflagellate symbionts. How might such "coral bleaching" affect corals and other species?
4. **MAKE CONNECTIONS** The bacterium *Wolbachia* is a symbiont that lives in mosquito cells and spreads rapidly through mosquito populations. *Wolbachia* can make mosquitoes resistant to infection by *Plasmodium*; researchers are seeking a strain that confers resistance and does not harm mosquitoes. Compare evolutionary changes that could occur if malaria control is attempted using such a *Wolbachia* strain versus using insecticides to kill mosquitoes. (Review Figure 28.18 and Concept 23.4.)

For suggested answers, see Appendix A.

▼ Figure 28.32 Effects of climate change on marine producers.



(a) Researchers studied 10 ocean regions, identified with letters on the map [see (b) for the corresponding names]. SSTs have increased since 1950 in most areas of these regions.



(b) The concentration of chlorophyll, an index for the biomass and growth of marine producers, has decreased over the same time period in most ocean regions.

28 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

SUMMARY OF KEY CONCEPTS

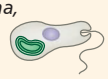
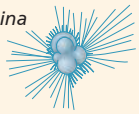
To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

CONCEPT 28.1

Most eukaryotes are single-celled organisms *(pp. 594–597)*

- Domain Eukarya includes many groups of **protists**, along with plants, animals, and fungi. Unlike prokaryotes, protists and other eukaryotes have a nucleus and other membrane-enclosed organelles, as well as a cytoskeleton that enables them to have asymmetric forms and to change shape as they feed, move, or grow.
- Protists are structurally and functionally diverse and have a wide variety of life cycles. Most are unicellular. Protists include photoautotrophs, heterotrophs, and **mixotrophs**.
- Current evidence indicates that eukaryotes originated by **endosymbiosis** when an archaeal host (or a host closely related to the archaea) engulfed an alpha proteobacterium that would evolve into an organelle found in all eukaryotes, the mitochondrion.
- Plastids are thought to be descendants of cyanobacteria that were engulfed by early eukaryotic cells. The plastid-bearing lineage eventually evolved into **red algae** and **green algae**. Other protist groups evolved from **secondary endosymbiotic** events in which red algae or green algae were themselves engulfed.
- In one hypothesis, eukaryotes are grouped into four supergroups: **Excavata, SAR, Archaeplastida**, and **Unikonta**.

? *Describe similarities and differences between protists and other eukaryotes.*

Key Concept/Eukaryote Supergroup	Major Groups	Key Morphological Characteristics	Specific Examples
CONCEPT 28.2 **Excavates include protists with modified mitochondria and protists with unique flagella** *(pp. 597–601)* ? *What evidence indicates that the excavates form a clade?*	**Diplomonads and parabasalids**	Modified mitochondria	*Giardia, Trichomonas* 
	Euglenozoans Kinetoplastids Euglenids	Spiral or crystalline rod inside flagella	*Trypanosoma, Euglena* 
CONCEPT 28.3 **SAR is a highly diverse group of protists defined by DNA similarities** *(pp. 601–609)* ? *Although they are not photosynthetic, apicomplexan parasites such as* Plasmodium *have modified plastids. Describe a current hypothesis that explains this observation.*	**Stramenopiles** Diatoms Oomycetes Brown algae	Hairy and smooth flagella	*Phytophthora, Laminaria* 
	Alveolates Dinoflagellates Apicomplexans Ciliates	Membrane-enclosed sacs (alveoli) beneath plasma membrane	*Pfiesteria, Plasmodium, Paramecium* 
	Rhizarians Radiolarians Forams Cercozoans	Amoebas with threadlike pseudopodia	*Globigerina* 
CONCEPT 28.4 **Red algae and green algae are the closest relatives of plants** *(pp. 609–611)* ? *On what basis do systematists place plants in the same supergroup (Archaeplastida) as red and green algae?*	**Red algae**	Phycoerythrin (photosynthetic pigment)	*Porphyridium, Palmaria* 
	Green algae	Plant-type chloroplasts	*Chlamydomonas, Ulva* 
	Plants	(See Chapters 29 and 30.)	Mosses, ferns, conifers, flowering plants 
CONCEPT 28.5 **Unikonts include protists that are closely related to fungi and animals** *(pp. 611–614)* ? *Describe a key feature for each of the main protist subgroups of Unikonta.*	**Amoebozoans** Tubulinids Slime molds Entamoebas	Amoebas with lobe-shaped or tube-shaped pseudopodia	*Amoeba, Dictyostelium* 
	Opisthokonts	(Highly variable; see Chapters 31–34.)	Choanoflagellates, nucleariids, animals, fungi 

CONCEPT 28.6

Protists play key roles in ecological communities *(pp. 614–615)*

- Protists form mutualistic and parasitic relationships that affect their symbiotic partners and many other members of the community.
- Photosynthetic protists are among the most important **producers** in aquatic communities. Because they are at the base of the food web, factors that affect photosynthetic protists affect many other species in the community.

? *Describe several protists that are ecologically important.*

TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

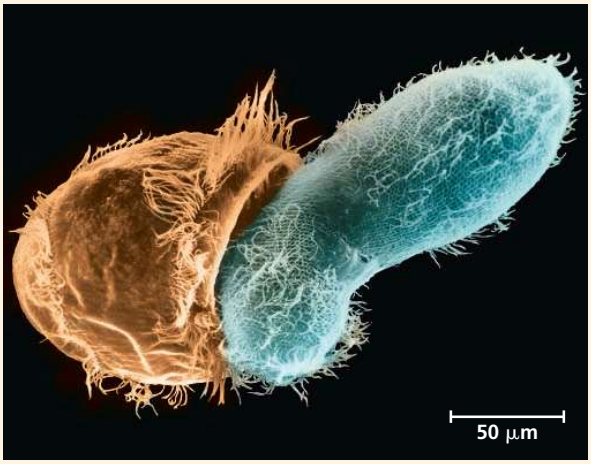
1. Plastids that are surrounded by more than two membranes are evidence of
   (A) evolution from mitochondria.
   (B) fusion of plastids.
   (C) origin of the plastids from archaea.
   (D) secondary endosymbiosis.
2. Biologists think that endosymbiosis gave rise to mitochondria before plastids partly because
   (A) the products of photosynthesis could not be metabolized without mitochondrial enzymes.
   (B) all eukaryotes have mitochondria (or their remnants), whereas many eukaryotes do not have plastids.
   (C) mitochondrial DNA is less similar to prokaryotic DNA than is plastid DNA.
   (D) without mitochondrial CO_2 production, photosynthesis could not occur.
3. Which group is correctly paired with its description?
   (A) diatoms—important consumers in aquatic communities
   (B) diplomonads—protists with modified mitochondria
   (C) apicomplexans—producers with intricate life cycles
   (D) red algae—acquired plastids by secondary endosymbiosis
4. According to the phylogeny presented in this chapter, which protists are in the same eukaryotic supergroup as plants?
   (A) green algae
   (B) dinoflagellates
   (C) red algae
   (D) both A and C
5. In a life cycle with alternation of generations, multicellular haploid forms alternate with
   (A) unicellular haploid forms.
   (B) unicellular diploid forms.
   (C) multicellular haploid forms.
   (D) multicellular diploid forms.

Levels 3-4: Applying/Analyzing

6. Based on the phylogenetic tree in Figure 28.5, which of the following statements is correct?
   (A) Excavata and SAR form a sister group.
   (B) The most recent common ancestor of SAR is older than that of Unikonta.
   (C) The most basal (first to diverge) eukaryotic supergroup cannot be determined.
   (D) Excavata is the most basal eukaryotic supergroup.
7. **EVOLUTION CONNECTION • DRAW IT** Medical researchers seek to develop drugs that can kill or restrict the growth of human pathogens yet have few harmful effects on patients. These drugs often work by disrupting the metabolism of the pathogen or by targeting its structural features.
   Draw and label a phylogenetic tree that includes an ancestral prokaryote and the following groups of organisms: Excavata, SAR, Archaeplastida, Unikonta, and, within Unikonta, amoebozoans, animals, choanoflagellates, fungi, and nucleariids. Based on this tree, hypothesize whether it would be most difficult to develop drugs to combat human pathogens that are prokaryotes, protists, animals, or fungi. (You do not need to consider the evolution of drug resistance by the pathogen.)

Levels 5-6: Evaluating/Creating

8. **SCIENTIFIC INQUIRY** Applying the "If … then" logic of deductive reasoning (see Concept 1.3), what are a few of the predictions that arise from the hypothesis that plants evolved from green algae? Put another way, how could you test this hypothesis?
9. **WRITE ABOUT A THEME: INTERACTIONS** Organisms interact with each other and the physical environment. In a short essay (100–150 words), explain how the response of diatom populations to a drop in nutrient availability can affect both other organisms and aspects of the physical environment (such as carbon dioxide concentrations).
10. **SYNTHESIZE YOUR KNOWLEDGE**



This micrograph shows a single-celled eukaryote, the ciliate *Didinium* (left), about to engulf its *Paramecium* prey, which is also a ciliate. Identify the eukaryotic supergroup to which ciliates belong and describe the role of endosymbiosis in the evolutionary history of that supergroup. Are these ciliates more closely related to all other protists than they are to plants, fungi, or animals? Explain.

For selected answers, see Appendix A.

29 Plant Diversity I: How Plants Colonized Land

KEY CONCEPTS

29.1 **Plants evolved from green algae** *p. 619*

29.2 **Mosses and other nonvascular plants have life cycles dominated by gametophytes** *p. 623*

29.3 **Ferns and other seedless vascular plants were the first plants to grow tall** *p. 629*

Study Tip

Make a table: As you read the chapter, make a table of adaptations for life on land that evolved in plants after they diverged from their close aquatic relatives, a group of charophyte algae.

Adaptation	Description	How it facilitates life on land
Cuticle	Waxy covering on outer body surface	Reduces dessication

Go to Mastering Biology

For Students (in eText and Study Area)
- Get Ready for Chapter 29
- Animation: Moss Life Cycle
- Animation: Fern Life Cycle

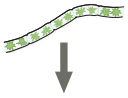
For Instructors to Assign (in Item Library)
- Visualizing the Concept: Haploid and Diploid Generations Alternate in Plant Life Cycles
- Scientific Skills Exercise: Making Bar Graphs and Interpreting Data



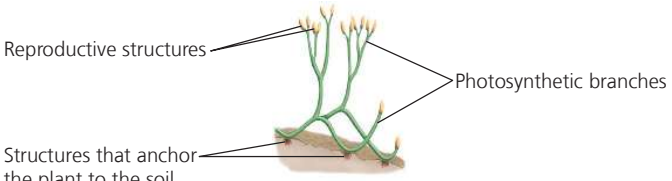
Figure 29.1 For much of Earth's history, the land surface was largely lifeless. Some prokaryotes lived on land 3.2 billion years ago, but it was only within the last 500 million years that small plants, fungi, and animals joined them ashore. Finally, by 385 million years ago, the first forests appeared (but with different species than those of today).

What were the major developments in the evolution of plants?

Plants originated from green algae about 470 million years ago.



By 425 million years ago, some early plants had **traits facilitating life on land.**



Over time, early plants gave rise to a **rich diversity of plants.**



Nonvascular plants (such as mosses)

Seedless vascular plants (such as ferns)

Seed plants (cone-bearing plants and flowering plants)

CONCEPT 29.1

Plants evolved from green algae

Today, there are more than 325,000 known plant species. Although a few plant species returned to aquatic habitats during their evolution, most present-day plants live on land. In this text, we distinguish plants from algae, which are photosynthetic protists.

Plants enabled other life-forms to survive on land. For example, plants supply oxygen and are a key source of food for terrestrial animals. Also, by their very presence, plants such as the trees of a forest physically create the habitats required by animals and many other organisms.

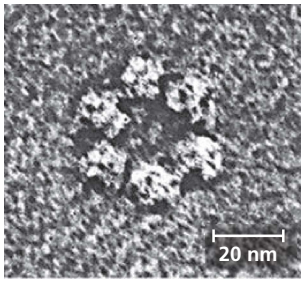
As you read in Concept 28.4, green algae called charophytes are the closest relatives of plants. We'll begin with a closer look at the evidence for this relationship.

Evidence of Algal Ancestry

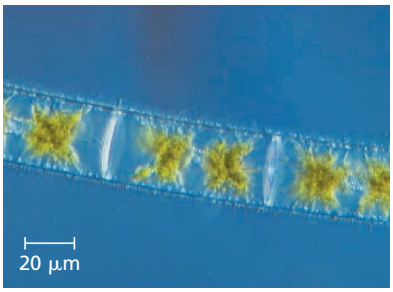
Many key traits of plants are found in some algae. For example, plants are multicellular, eukaryotic, photosynthetic autotrophs, as are brown, red, and certain green algae. Plants have cell walls made of cellulose, and so do green algae, dinoflagellates, and brown algae. And chloroplasts with chlorophylls *a* and *b* are present in green algae, euglenids, and a few dinoflagellates, as well as in plants.

However, the charophytes are the only present-day algae that share certain distinctive traits with plants, suggesting that they are the closest living relatives of plants. For example, the cells of both plants and charophytes have distinctive circular rings of proteins embedded in the plasma membrane **(Figure 29.2)**; these protein rings synthesize the cellulose found in the cell wall. In contrast, noncharophyte algae have linear sets of proteins that synthesize cellulose. Likewise, in species of plants that have flagellated sperm, the structure of the sperm closely resembles that of charophyte sperm. Analyses of nuclear, chloroplast, and mitochondrial DNA also support the close relationship between plants and charophytes.

▼ **Figure 29.2 Rings of cellulose-synthesizing proteins.** (inverted-contrast TEM)



More specifically, a recent analysis of nearly 900 protein-coding nuclear genes found that charophytes in the clade Zygnematophyceae—such as *Zygnema*—are the closest living relatives of plants **(Figure 29.3)**. Although this evidence shows that plants arose from within a group of charophyte algae, it does not mean that plants are descended from these living algae. Even so, present-day charophytes may tell us something about the algal ancestors of plants.



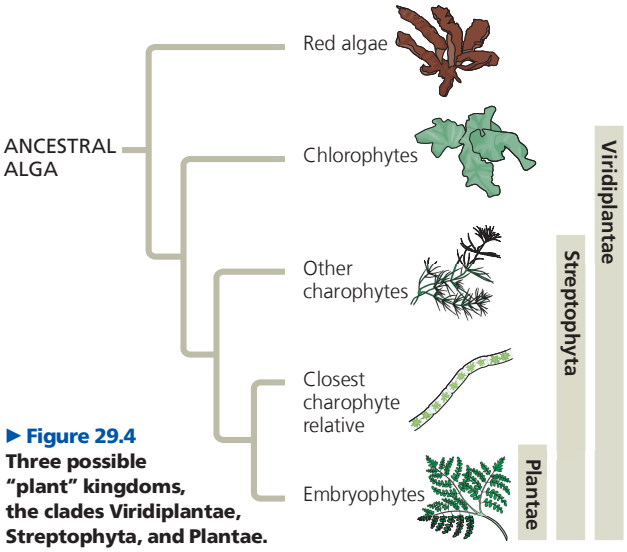
▶ **Figure 29.3 *Zygnema*, an alga closely related to plants.** *Zygnema* is a filamentous pond alga in the Zygnematophyceae, the group of charophytes that is most closely related to plants.

Adaptations Enabling the Move to Land

Many species of charophyte algae inhabit shallow waters around the edges of ponds and lakes, where they are subject to occasional drying. In such environments, natural selection favors individual algae that can survive periods when they are not submerged. In charophytes, a layer of a durable polymer called **sporopollenin** prevents exposed zygotes from drying out. A similar chemical adaptation is found in the tough sporopollenin walls that encase plant spores.

The accumulation of such traits by at least one population of charophyte algae (now extinct) enabled their descendants—the first plants—to live permanently above the waterline. This ability opened a new frontier: a terrestrial habitat that offered enormous benefits. The bright sunlight was unfiltered by water and plankton; the atmosphere offered more plentiful carbon dioxide than did water; and the soil by the water's edge was rich in some mineral nutrients. But these benefits were accompanied by challenges: a relative scarcity of water and a lack of structural support against gravity. (To appreciate why such support is important, picture how the soft body of a jellyfish (jelly) collapses when waves strand it on a beach.) Plants diversified as new adaptations arose that enabled them to thrive despite these challenges.

Today, what adaptations are unique to plants? The answer depends on where you draw the boundary dividing plants from algae **(Figure 29.4)**. Since the placement of this



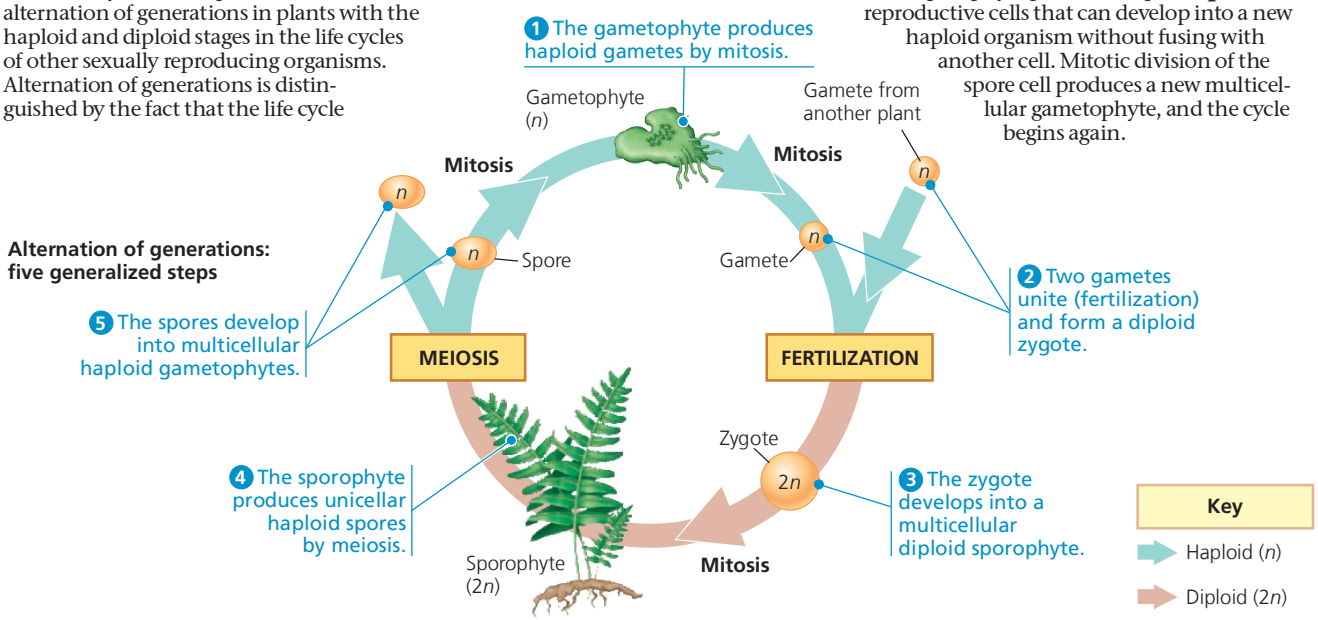
▶ **Figure 29.4 Three possible "plant" kingdoms, the clades Viridiplantae, Streptophyta, and Plantae.**

▼ Figure 29.5 Exploring Alternation of Generations

Charophyte algae lack the key traits of plants described in this figure: alternation of generations and the associated trait of multicellular, dependent embryos. As described in the main text, charophyte algae also lack walled spores produced in sporangia and apical meristems. This suggests that these four traits were absent in the ancestor common to plants and charophytes but instead evolved as derived traits of plants. Not every plant exhibits all of these traits: Certain lineages of plants have lost some traits over time.

Alternation of Generations

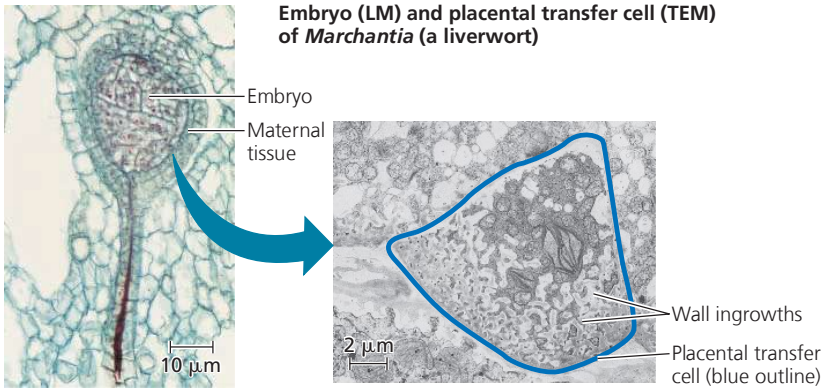
The life cycles of all plants alternate between two generations of distinct multicellular organisms: gametophytes and sporophytes. As shown in the diagram below (using a fern as an example), each generation gives rise to the other, a process that is called **alternation of generations**. This type of reproductive cycle evolved in various groups of algae but does not occur in the charophytes, the algae most closely related to plants. Take care not to confuse the alternation of generations in plants with the haploid and diploid stages in the life cycles of other sexually reproducing organisms. Alternation of generations is distinguished by the fact that the life cycle includes both multicellular haploid organisms and multicellular diploid organisms. The multicellular haploid **gametophyte** ("gamete-producing plant") is named for its production by mitosis of haploid gametes—eggs and sperm—that fuse during fertilization, forming diploid zygotes. Mitotic division of the zygote produces a multicellular diploid **sporophyte** ("spore-producing plant"). Meiosis in a mature sporophyte produces haploid **spores**, reproductive cells that can develop into a new haploid organism without fusing with another cell. Mitotic division of the spore cell produces a new multicellular gametophyte, and the cycle begins again.



Multicellular, Dependent Embryos

As part of a life cycle with alternation of generations, multicellular plant embryos develop from zygotes that are retained within the tissues of the female parent (a gametophyte). The parental tissues protect the developing embryo from harsh environmental conditions and provide nutrients such as sugars and amino acids. The embryo has specialized *placental transfer cells* that enhance the transfer of nutrients to the embryo through elaborate ingrowths of the wall surface (plasma membrane and cell wall). The multicellular, dependent embryo of plants is such a significant derived trait that plants are also known as **embryophytes**.

Embryo (LM) and placental transfer cell (TEM) of *Marchantia* (a liverwort)



MAKE CONNECTIONS *Review sexual life cycles in Figure 13.6. Identify which type of sexual life cycle has alternation of generations, and summarize how it differs from other life cycles.*

boundary is the subject of ongoing debate, this text uses a traditional definition that equates the kingdom Plantae with embryophytes (plants with embryos). In this context, let's now examine the derived traits that separate plants from their closest algal relatives.

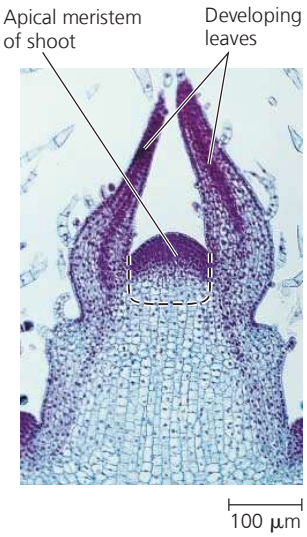
Derived Traits of Plants

Several adaptations that facilitate survival and reproduction on dry land emerged after plants diverged from their algal relatives. Examples of such traits that are found in plants but not in charophyte algae include the following:

- **Alternation of generations.** This type of life cycle, consisting of multicellular forms that give rise to each other in turn, is described in **Figure 29.5**.
- **Walled spores produced in sporangia.** The sporophyte stage of the plant life cycle has multicellular organs called **sporangia** (singular, *sporangium*) that produce spores **(Figure 29.6)**. The polymer sporopollenin makes the walls of these spores resistant to harsh environments, enabling plant spores to be dispersed through dry air without harm.
- **Apical meristems.** Plants also differ from their algal relatives in having **apical meristems**, localized regions of cell division at the tips of roots and shoots **(Figure 29.7)**. Apical meristem cells can divide throughout the plant's life, enabling its roots and shoots to elongate, thus increasing the plant's exposure to environmental resources.

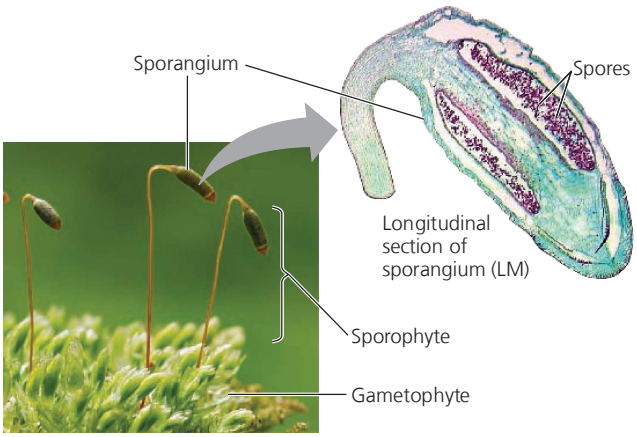
Additional derived traits that relate to terrestrial life have evolved in many plant species. For example, the epidermis in many species has a covering, the **cuticle**, which consists of wax and other polymers. Permanently exposed to the air, plants run a far greater risk of desiccation (drying out) than do their algal relatives. The cuticle acts as waterproofing, helping prevent excessive water loss from the aboveground plant organs, while also providing some protection from microbial attack. Most plants also have specialized pores called **stomata** (singular, *stoma*), which support photosynthesis by allowing the exchange of CO_2 and O_2 between the outside air and the plant (see Figure 10.3). Stomata are also the main avenues by which water evaporates from the plant; in hot, dry conditions, the stomata close, minimizing water loss.

The earliest plants lacked true roots and leaves. Without roots, how did these plants absorb nutrients from the soil? Fossils dating from 420 million years ago reveal an adaptation that may have aided early plants in nutrient uptake: They formed symbiotic associations with fungi. We'll explore these associations, called *mycorrhizae*, and their benefits to both plants and fungi in more detail in Concept 31.1. For now, the main point is that mycorrhizal fungi form extensive networks of filaments through the soil and transfer nutrients to their symbiotic plant partner. This benefit may have helped plants without roots to colonize land.



◀ Figure 29.7 Apical meristem of a plant shoot. Cells produced by apical meristems differentiate into the outer epidermis, which protects the body, and various types of internal tissues, such as those in leaves (LM).

▼ Figure 29.6 Sporophytes and sporangia of a moss in the genus *Mnium*. Each of the many spores produced by a sporangium is encased by a durable, sporopollenin-enriched wall.



The Origin and Diversification of Plants

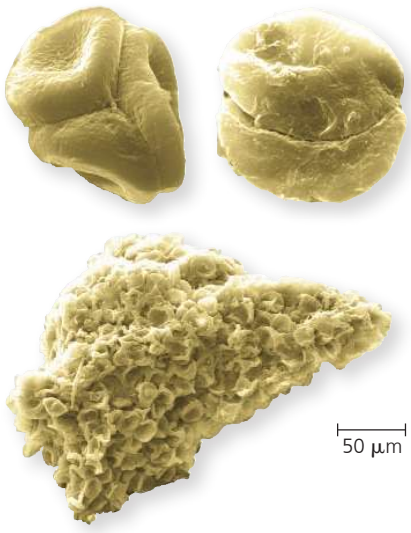
The algae most closely related to plants include many unicellular species and small colonial species. Since it is likely that the first plants were similarly small, the search for the earliest fossils of plants has focused on the microscopic world. As mentioned earlier, microorganisms colonized land as early as 3.2 billion years ago. But the microscopic fossils that document life on land changed dramatically 470 million years ago with the appearance of spores from early plants.

What distinguishes these spores from those of algae or fungi? One clue comes from their chemical composition, which matches the composition of plant spores today but differs from that of the spores of other organisms. In addition, the walls of these ancient spores have structural features that today are found only in the spores of certain plants (liverworts). And in rocks dating to 450 million years ago,

▼ **Figure 29.8 Ancient plant spores and tissue.** (colorized SEMs)

(a) Fossilized spores. The chemical composition and the physical structure of the walls of these 450-million-year-old spores match those found in certain plants today.

(b) Fossilized sporophyte tissue. The spores in (a) were embedded in tissue that appears to be from plants.



researchers have discovered similar spores embedded in plant cuticle material that resembles spore-bearing tissue in living plants **(Figure 29.8)**.

Fossils of larger plant structures, such as the *Cooksonia* sporangium in **Figure 29.9**, date to 425 million years ago, which is 45 million years after the appearance of plant spores in the fossil record. While the precise age (and form) of the first plants has yet to be discovered, those ancestral species gave rise to the vast diversity of living plants. **Table 29.1** provides basic information about the ten extant phyla. (Extant lineages are those that have surviving members.) As you read the rest of this section, look at Table 29.1 together with **Figure 29.10**, which reflects a view of plant phylogeny that is based on plant anatomy, biochemistry, and genetics.

One way to distinguish groups of plants is whether or not they have an extensive system of **vascular tissue**, cells joined into tubes that transport water and nutrients throughout the plant body. Most present-day plants have a complex vascular tissue system and are therefore called **vascular plants**. Plants that do not have an extensive transport system—liverworts, mosses, and hornworts—are described as "nonvascular" plants, even though some mosses do have simple vascular tissue. Nonvascular plants are often informally called **bryophytes** (from the Greek *bryon*, moss, and *phyton*, plant). Although the term *bryophyte* is commonly used to refer to all nonvascular plants, molecular studies and morphological analyses of sperm structure have concluded that bryophytes do not form a monophyletic group (a clade).



▶ **Figure 29.9 *Cooksonia* sporangium fossil.** With the exception of the shape of its sporangia, *Cooksonia*'s overall form was very similar to the early plant shown in Figures 29.1 and 29.16.

Table 29.1 Ten Phyla of Extant Plants

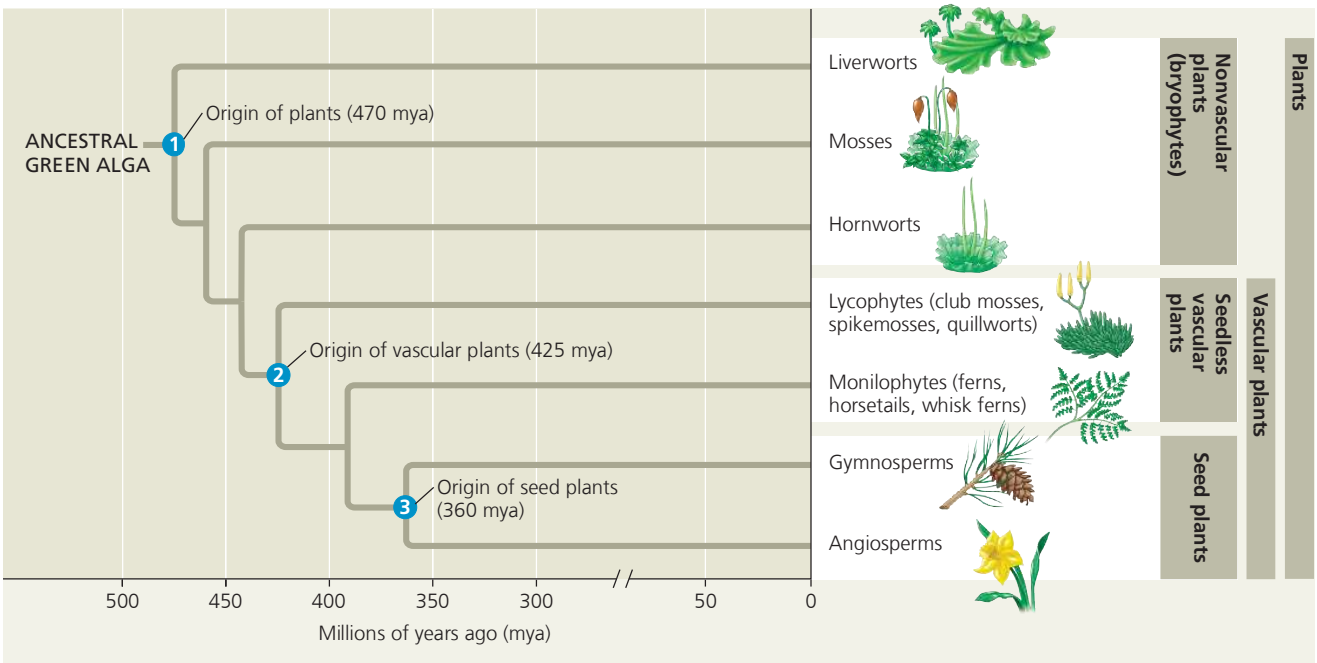
	Common Name	Number of Known Species
Nonvascular Plants (Bryophytes)		
Phylum Hepatophyta	Liverworts	9,000
Phylum Bryophyta	Mosses	13,000
Phylum Anthocerophyta	Hornworts	225
Vascular Plants		
Seedless Vascular Plants		
Phylum Lycophyta	Lycophytes	1,200
Phylum Monilophyta	Monilophytes	12,000
Seed Plants		
Gymnosperms		
Phylum Ginkgophyta	Ginkgo	1
Phylum Cycadophyta	Cycads	350
Phylum Gnetophyta	Gnetophytes	75
Phylum Coniferophyta	Conifers	600
Angiosperms		
Phylum Anthophyta	Flowering plants	290,000

Vascular plants, which form a clade that comprises about 93% of all extant plant species, can be categorized further into smaller clades. Two of these clades are the **lycophytes** (the club mosses and their relatives) and the **monilophytes** (ferns and their relatives). The plants in each of these clades lack seeds, which is why collectively the two clades are informally called **seedless vascular plants**. However, notice in Figure 29.10 that, like bryophytes, seedless vascular plants do not form a clade.

A group such as the bryophytes or the seedless vascular plants represents a collection of organisms that share key biological features. It can be informative to group organisms according to their features, such as having a vascular system but lacking seeds. But members of such a group, unlike members of a clade, do not necessarily share the same ancestry. For example, even though monilophytes and lycophytes are all seedless vascular plants, monilophytes share a more recent common ancestor with seed plants. As a result, we would expect monilophytes and seed plants to share key traits not found in lycophytes—and they do, as you'll read in Concept 29.3.

A third clade of vascular plants consists of seed plants, which represent the vast majority of living plant species.

▼ Figure 29.10 Highlights of plant evolution. The phylogeny shown here illustrates a leading hypothesis about the relationships between plant groups.



MAKE CONNECTIONS *The figure identifies which lineages are plants, nonvascular plants, vascular plants, seedless vascular plants, and seed plants. Which of these categories are monophyletic, and which are paraphyletic? Explain. (See Figure 26.10 to review these terms.)*

A **seed** is an embryo packaged with a supply of nutrients inside a protective coat. Seed plants can be divided into two groups, gymnosperms and angiosperms, based on the absence or presence of enclosed chambers in which seeds mature. **Gymnosperms** (from the Greek *gymnos*, naked, and *sperm*, seed) are known as "naked seed" plants because their seeds are not enclosed in chambers. Living gymnosperm species, the most familiar of which are the conifers, form a clade. **Angiosperms** (from the Greek *angion*, container) are a huge clade consisting of all flowering plants; their seeds develop inside chambers that originate within flowers. Nearly 90% of living plant species are angiosperms.

Note that the phylogeny depicted in Figure 29.10 focuses only on the relationships between extant plant lineages. Paleobotanists have also discovered fossils belonging to extinct plant lineages. As you'll read later in the chapter, these fossils can reveal intermediate steps in the emergence of plant groups found on Earth today.

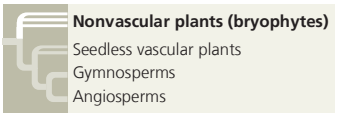
CONCEPT CHECK 29.1

1. Why do researchers identify the charophytes rather than another group of algae as the closest living relatives of plants?
2. Identify four derived traits that distinguish plants from charophyte green algae and facilitate life on land. Explain.
3. **WHAT IF?** What would the human life cycle be like if we had alternation of generations? Assume that the multicellular diploid stage would be similar in form to an adult human.

For suggested answers, see Appendix A.

CONCEPT 29.2

Mosses and other nonvascular plants have life cycles dominated by gametophytes



The nonvascular plants (bryophytes) are represented today by three phyla of small, herbaceous (nonwoody) plants: **liverworts** (phylum Hepatophyta), **mosses** (phylum Bryophyta), and **hornworts** (phylum Anthocerophyta). Liverworts and hornworts are named for their shapes, plus the suffix *wort* (from the Anglo-Saxon for "herb"). Mosses are familiar to many people, although some plants commonly called "mosses" are not really mosses at all. These include Irish moss (a red seaweed), reindeer moss (a lichen), club mosses (seedless vascular plants), and Spanish mosses (lichens in some regions and flowering plants in others).

Phylogenetic analyses indicate that liverworts, mosses, and hornworts diverged from other plant lineages early in the history of plant evolution (see Figure 29.10). Fossil evidence provides some support for this idea: The earliest spores of plants (dating from 450 to 470 million years ago) have structural features found only in the spores of

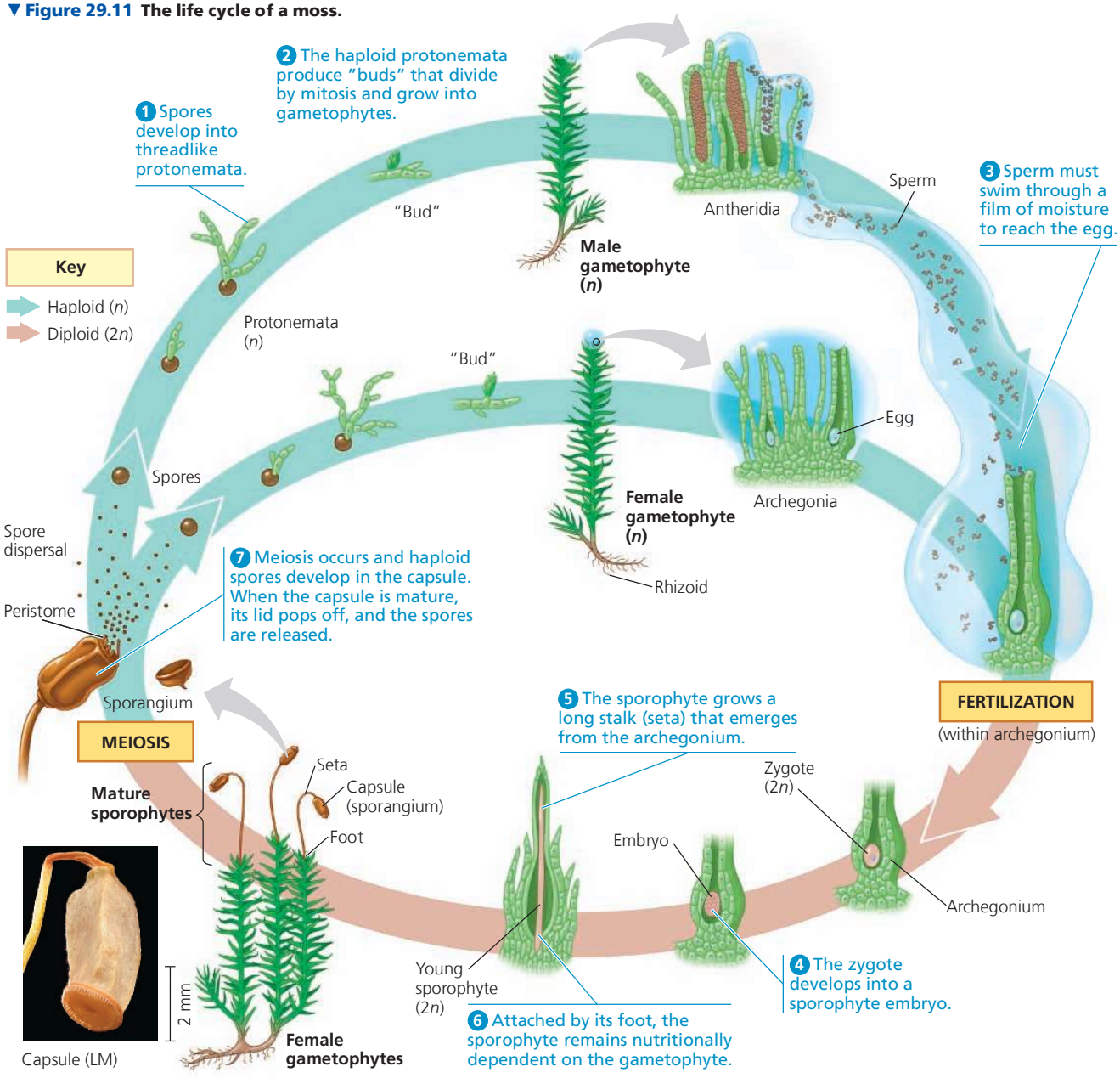
liverworts, and by 430 million years ago spores similar to those of mosses and hornworts also occur in the fossil record. The earliest fossils of vascular plants date to about 425 million years ago.

Over the long course of their evolution, liverworts, mosses, and hornworts have acquired many unique adaptations. Next, we'll examine some of those features.

Bryophyte Gametophytes

Unlike vascular plants, in all three bryophyte phyla the haploid gametophytes are the dominant stage of the life cycle: They are usually larger and longer-living than the sporophytes, as shown in the moss life cycle in **Figure 29.11**. The sporophytes are typically present only part of the time.

▼ Figure 29.11 The life cycle of a moss.



VISUAL SKILLS *In this diagram, does the sperm cell that fertilizes the egg cell differ genetically from the egg? Explain.*

Mastering Biology Animation: Moss Life Cycle

When bryophyte spores are dispersed to a favorable habitat, such as moist soil or tree bark, they may germinate and grow into gametophytes. Germinating moss spores, for example, characteristically produce a mass of green, branched, one-cell-thick filaments known as a **protonema** (plural, *protonemata*). A protonema has a large surface area that enhances absorption of water and minerals. In favorable conditions, a protonema produces one or more "buds," each of which develops into a moss gametophyte. (Note that when referring to nonvascular plants, we often use quotation marks for structures similar to the buds, stems, and leaves of vascular plants because the definitions of these terms are based on vascular plant organs.)

Bryophyte gametophytes generally form ground-hugging carpets, partly because their body parts are too thin to support a tall plant. A second constraint on the height of many bryophytes is the absence of vascular tissue, which would enable long-distance transport of water and nutrients. (The thin structure of bryophyte organs makes it possible to distribute materials for short distances without specialized vascular tissue.) However, some mosses have conducting tissues in the center of their "stems." A few of these mosses can grow as tall as 60 cm (2 feet) as a result. Phylogenetic analyses suggest that conducting tissues similar to those of vascular plants arose independently in these mosses by convergent evolution.

The gametophytes are anchored to the ground by delicate **rhizoids**, which are long, tubular single cells (in liverworts and hornworts) or filaments of cells (in mosses). Unlike roots, which are found in vascular plant sporophytes, rhizoids lack specialized conducting cells and do not play a primary role in water and mineral absorption.

Gametophytes can form multiple **gametangia**, multicellular structures that produce gametes and are covered by protective tissue. Female gametangia are called **archegonia**, and male gametangia are called **antheridia**. Each archegonium produces one egg, whereas each antheridium produces many sperm. Some bryophyte gametophytes are bisexual, but in mosses the archegonia and antheridia are typically carried on separate female and male gametophytes. Flagellated sperm swim through a film of water toward eggs, entering the archegonia in response to chemical attractants. Eggs are not released but instead remain within the bases of archegonia. After fertilization, embryos are retained within the archegonia. Layers of placental transfer cells help transport nutrients to the embryos as they develop into sporophytes.

Bryophyte sperm typically require a film of water to reach the eggs. Given this requirement, it is not surprising that many bryophyte species are found in moist habitats. The fact that sperm swim through water to reach the egg also means that in species with separate male and female gametophytes (most species of mosses), sexual reproduction is likely to be more successful when individuals are located close to one another.



▶ Figure 29.12 A moss brood body.

Many bryophyte species can increase the number of individuals in a local area through various methods of asexual reproduction. For example, some mosses reproduce asexually by forming *brood bodies*, small plantlets that detach from the parent plant and grow into new, genetically identical copies of their parent **(Figure 29.12)**.

Bryophyte Sporophytes

The cells of bryophyte sporophytes contain plastids that are usually green and photosynthetic when the sporophytes are young. Even so, bryophyte sporophytes cannot live independently. A bryophyte sporophyte remains attached to its parental gametophyte throughout the sporophyte's lifetime, dependent on the gametophyte for supplies of sugars, amino acids, minerals, and water.

Bryophytes have the smallest sporophytes of all extant plant groups. A typical bryophyte sporophyte consists of a foot, a seta, and a sporangium. Embedded in the archegonium, the **foot** absorbs nutrients from the gametophyte. The **seta** (plural, *setae*), or stalk, conducts these materials to the sporangium, also called a **capsule**, which produces spores by meiosis.

Bryophyte sporophytes can produce enormous numbers of spores. A single moss capsule, for example, can generate over 5 million spores. In most mosses, the seta becomes elongated, enhancing spore dispersal by elevating the capsule. Typically, the upper part of the capsule features a ring of interlocking, tooth-like structures known as the **peristome** (see Figure 29.11). These "teeth" open under dry conditions and close again when it is moist. This allows moss spores to be discharged gradually, via periodic gusts of wind that can carry them long distances.

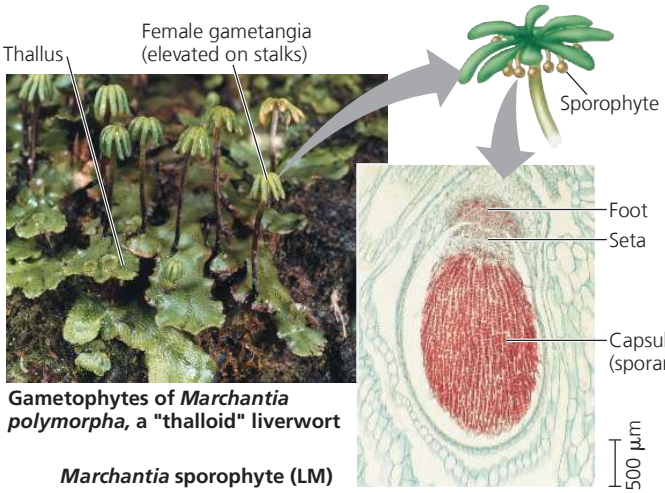
Moss and hornwort sporophytes are often larger and more complex than those of liverworts. For example, hornwort sporophytes, which superficially resemble grass blades, have a cuticle. Moss and hornwort sporophytes also have stomata, as do all vascular plants (but not liverworts).

Figure 29.13 shows some examples of gametophytes and sporophytes in the bryophyte phyla.

▼ Figure 29.13 Exploring Bryophyte Diversity

Liverworts (Phylum Hepatophyta)

This phylum's common and scientific names (from the Latin *hepaticus*, liver) refer to the liver-shaped gametophytes of its members, such as *Marchantia*, shown below. In medieval times, their shape was thought to be a sign that the plants could help treat liver diseases. Some liverworts, including *Marchantia*, are described as "thalloid" because of the flattened shape of their gametophytes. *Marchantia* gametangia are elevated on stalks that look like miniature trees. You would need a magnifying glass to see the sporophytes, which have a short seta (stalk) with an oval or round capsule. Other liverworts, such as *Plagiochila*, below, are called "leafy" because their stemlike gametophytes have many leaflike appendages. There are many more species of leafy liverworts than thalloid liverworts.



Gametophytes of *Marchantia polymorpha*, a "thalloid" liverwort

***Marchantia* sporophyte (LM)**



***Plagiochila deltoidea*, a "leafy" liverwort**

Hornworts (Phylum Anthocerophyta)

This phylum's common and scientific names (from the Greek *keras*, horn) refer to the long, tapered shape of the sporophyte. A typical sporophyte can grow to about 5 cm high. Unlike a liverwort or moss sporophyte, a hornwort sporophyte lacks a seta and consists only of a sporangium. The sporangium releases mature spores by splitting open, starting at the tip of the horn. The gametophytes, which are usually 1–2 cm in diameter, grow mostly horizontally and often have multiple sporophytes attached. Hornworts are frequently among the first species to colonize open areas with moist soils; a symbiotic relationship with nitrogen-fixing cyanobacteria contributes to their ability to do this (nitrogen is often in short supply in such areas).

An *Anthoceros* hornwort species



Mosses (Phylum Bryophyta)

Moss gametophytes, which range in height from less than 1 mm to 60 cm, are less than 15 cm tall in most species. The familiar carpet of moss you observe consists mainly of gametophytes. The blades of their "leaves" are usually only one cell thick, but more complex "leaves" that have ridges coated with cuticle can be found on the common hairy-cap moss (*Polytrichum*, below) and its close relatives. Moss sporophytes are typically elongated and visible to the naked eye, with heights ranging up to about 20 cm. Though green and photosynthetic when young, they turn tan or brownish red when ready to release spores.



***Polytrichum commune*, hairy-cap moss**

The Ecological and Economic Importance of Mosses

Wind dispersal of lightweight spores has distributed mosses throughout the world. These plants are particularly common and diverse in moist forests and wetlands. Some mosses colonize bare, sandy soil, where, researchers have found, they help retain nitrogen in the soil **(Figure 29.14)**. In northern coniferous forests, species such as the feather moss *Pleurozium* harbor nitrogen-fixing cyanobacteria that increase the availability of nitrogen in the ecosystem. Other mosses inhabit such extreme environments as mountaintops, tundra, and deserts. Many mosses are able to live in very cold or dry habitats because they can survive the loss of most of their body water, then rehydrate when moisture is available. Few vascular plants can survive the same degree of desiccation. Moreover, phenolic compounds in moss cell walls absorb damaging levels of UV radiation present in deserts or at high altitudes.

One wetland moss genus, *Sphagnum*, or peat moss, is often a major component of deposits of partially decayed organic material known as **peat (Figure 29.15a)**. Boggy regions with thick layers of peat are called peatlands. *Sphagnum* does not decay readily, in part because of phenolic compounds embedded in its cell walls. The low temperature, pH, and oxygen level of peatlands also inhibit decay of moss and other organisms in these boggy wetlands. As a result, some peatlands have preserved corpses for thousands of years **(Figure 29.15b)**.

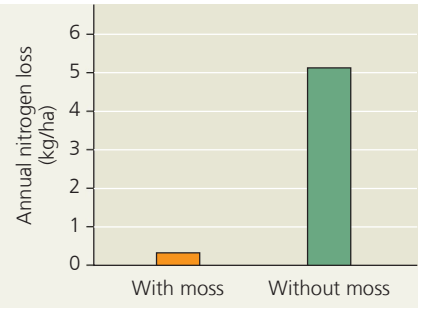
Peat has long been a fuel source in Europe and Asia, and it is still harvested for fuel today, notably in Ireland and

▼ Figure 29.14 Inquiry

Can bryophytes reduce the rate at which key nutrients are lost from soils?

Experiment Soils in terrestrial ecosystems are often low in nitrogen, a nutrient required for normal plant growth. Richard Bowden, of Allegheny College, measured annual inputs (gains) and outputs (losses) of nitrogen in a sandy soil ecosystem dominated by the moss *Polytrichum*. Nitrogen inputs were measured from rainfall (dissolved ions, such as nitrate, NO_3^-), biological N_2 fixation, and wind deposition. Nitrogen losses were measured in leached water (dissolved ions, such as NO_3^-) and gaseous emissions (such as N_2O emitted by bacteria). Bowden measured losses for soils with *Polytrichum* and for soils where the moss was removed two months before the experiment began.

Results A total of 10.5 kg of nitrogen per hectare (kg/ha) entered the ecosystem each year. Little nitrogen was lost by gaseous emissions [0.10 kg/(ha · yr)]. The results of comparing nitrogen losses by leaching are shown below.



Conclusion The moss *Polytrichum* greatly reduced the loss of nitrogen by leaching in this ecosystem. Each year, the moss ecosystem retained over 95% of the 10.5 kg/ha of total nitrogen inputs (only 0.1 kg/ha and 0.3 kg/ha were lost to gaseous emissions and leaching, respectively).

Data from R. D. Bowden, Inputs, outputs, and accumulation of nitrogen in an early successional moss (*Polytrichum*) ecosystem, *Ecological Monographs* 61:207–223 (1991).

WHAT IF? *How might the presence of* Polytrichum *affect plant species that typically colonize the sandy soils after the moss?*

▼ Figure 29.15 ***Sphagnum*, or peat moss: a bryophyte with economic, ecological, and archaeological significance.**



(a) Peat being harvested from a peatland



(b) "Tollund Man," a bog mummy dating from 405–100 BCE. The acidic, oxygen-poor conditions produced by *Sphagnum* can preserve human or other animal bodies for thousands of years.

Scientific Skills Exercise

Making Bar Graphs and Interpreting Data



Could Nonvascular Plants Have Caused Weathering of Rocks and Contributed to Climate Change During the Ordovician Period? The oldest traces of terrestrial plants are fossilized spores formed 470 million years ago. Between that time and the end of the Ordovician period 444 million years ago, the atmospheric CO_2 level dropped by half, and the climate cooled dramatically.

One possible cause of the drop in CO_2 during the Ordovician period is the breakdown, or weathering, of rock. As rock weathers, calcium silicate (Ca_2SiCO_3) is released and combines with CO_2 from the air, producing calcium carbonate ($CaCO_3$). Today, the roots of vascular plants increase rock weathering and mineral release by producing acids that break down rock and soil. Although nonvascular plants lack roots, they require the same mineral nutrients as vascular plants. Could nonvascular plants also increase the chemical weathering of rock? If so, they could have contributed to the decline in atmospheric CO_2 during the Ordovician. In this exercise, you will interpret data from a study of the effects of moss on releasing minerals from two types of rock.

How the Experiment Was Done The researchers set up experimental and control microcosms, or small artificial ecosystems, to measure mineral release from rocks. First, they placed rock fragments of volcanic origin, either granite or andesite, into small glass containers. Then they mixed water and macerated (chopped and crushed) moss of the species *Physcomitrella patens*. They added this mixture to the experimental microcosms (72 granite and 41 andesite). For the control microcosms (77 granite and 37 andesite), they filtered out the moss and just added the water. After 130 days, they measured the amounts of various minerals found in the water in the control microcosms and in the water and moss in the experimental microcosms.

Data from the Experiment The moss grew (increased its biomass) in the experimental microcosms. The table shows the mean amounts in micromoles (μmol) of several minerals measured in the water and the moss in the microcosms.

INTERPRET THE DATA

1. Why did the researchers add filtrate from which macerated moss had been removed to the control microcosms?
2. Make two bar graphs (for granite and andesite) comparing the mean amounts of each element weathered from rocks in the control and experimental microcosms. (Hint: For an experimental microcosm, what sum represents the total amount weathered from rocks?) (For additional information on bar graphs, see the Scientific Skills Review in Appendix D.)
3. Overall, what is the effect of moss on chemical weathering of rock? Are the results similar or different for granite and andesite?
4. Based on their experimental results, the researchers added weathering of rock by nonvascular plants to simulation models of the Ordovician climate. The new models predicted decreased CO_2 levels and global cooling sufficient to produce the glaciations in the late Ordovician period. What assumptions did the researchers make in using results from their experiments in climate simulation models?
5. "Life has profoundly changed the Earth." Explain whether or not these experimental results support this statement.

Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

	Ca^{2+} (μmol)		Mg^{2+} (μmol)		K^+ (μmol)	
	Granite	Andesite	Granite	Andesite	Granite	Andesite
Mean weathered amount released in water in the control microcosms	1.68	1.54	0.42	0.13	0.68	0.60
Mean weathered amount released in water in the experimental microcosms	1.27	1.84	0.34	0.13	0.65	0.64
Mean weathered amount taken up by moss in the experimental microcosms	1.09	3.62	0.31	0.56	1.07	0.28

Data from T. M. Lenton et al., First plants cooled the Ordovician, *Nature Geoscience* 5:86–89 (2012).

Canada. Peat moss is also useful as a soil conditioner and for packing plant roots during shipment because it has large dead cells that can absorb roughly 20 times the moss's weight in water.

Peatlands cover just 3% of Earth's land surface but contain one-third of the world's soil carbon: Globally, an estimated 500 billion tons of organic carbon is stored as peat. Current overharvesting of *Sphagnum*—primarily for use in peat-fired power stations—contributes to global warming by releasing stored CO_2. In addition, if global temperatures continue to rise, the water levels of some peatlands are expected to drop. Such a change would expose peat to air and cause it to decompose, thereby releasing additional stored CO_2 and contributing further to global warming. The historical and expected future effects of *Sphagnum* on the global climate underscore the importance of preserving and managing peatlands.

Mosses may have a long history of affecting climate change. In the **Scientific Skills Exercise**, you will explore the question of whether they did so during the Ordovician period by contributing to the weathering of rocks.

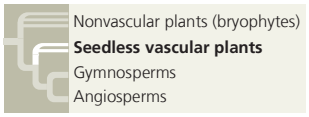
CONCEPT CHECK 29.2

1. How do bryophytes differ from other plants?
2. Give three examples of how structure fits function in bryophytes.
3. **MAKE CONNECTIONS** Review the discussion of feedback regulation in Concept 1.1. Could effects of global warming on peatlands alter CO_2 concentrations in ways that result in negative or positive feedback? Explain.

For suggested answers, see Appendix A.

CONCEPT 29.3

Ferns and other seedless vascular plants were the first plants to grow tall



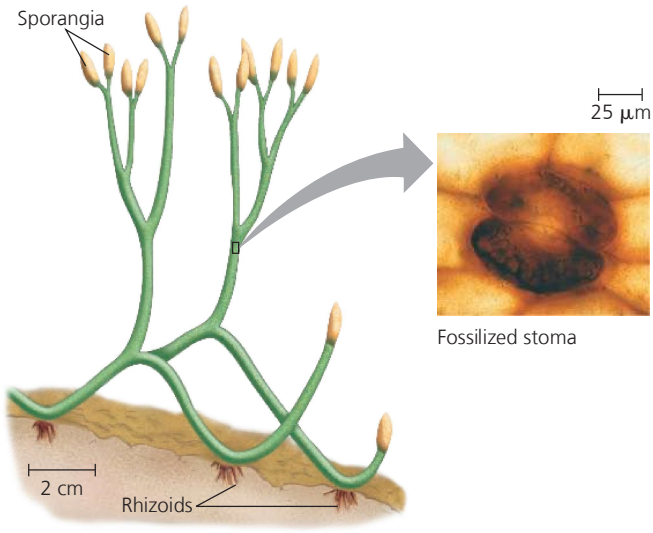
During the first 100 million years of plant evolution, bryophytes were prominent types of vegetation. But it is vascular plants that dominate most landscapes today. The earliest fossils of vascular plants date to 425 million years ago. These plants lacked seeds but had well-developed vascular systems, an evolutionary novelty that set the stage for vascular plants to grow taller than their bryophyte counterparts. As in bryophytes, however, the sperm of ferns and all other seedless vascular plants are flagellated and swim through a film of water to reach eggs. In part because of these swimming sperm, seedless vascular plants today are most common in damp environments.

Origins and Traits of Vascular Plants

Unlike the nonvascular plants, ancient relatives of vascular plants had branched sporophytes that were not dependent on gametophytes for nutrition **(Figure 29.16)**. Although these early plants were less than 20 cm tall, their branching enabled their bodies to become more complex and to have multiple sporangia. As plant bodies became more complex over time, competition for space and sunlight probably increased. As we'll see, that competition may have stimulated still more evolution in vascular plants, eventually leading to the formation of the first forests.

Early vascular plants had some derived traits of today's vascular plants, but they lacked roots and some other adaptations that evolved later. The main traits that characterize living vascular plants are life cycles with dominant sporophytes, transport in vascular tissues called xylem and phloem, and well-developed roots and leaves, including spore-bearing leaves called sporophylls.

▼ Figure 29.16 Sporophytes of *Aglaophyton major*, an ancient relative of living vascular plants. This reconstruction from 405-million-year-old fossils exhibits dichotomous (Y-shaped) branching with sporangia at the ends of branches. Sporophyte branching characterizes living vascular plants but is lacking in living nonvascular plants (bryophytes). *Aglaophyton* had structures called rhizoids that anchored it to the ground. The inset shows a fossilized stoma of *A. major* (colorized LM).



Life Cycles with Dominant Sporophytes

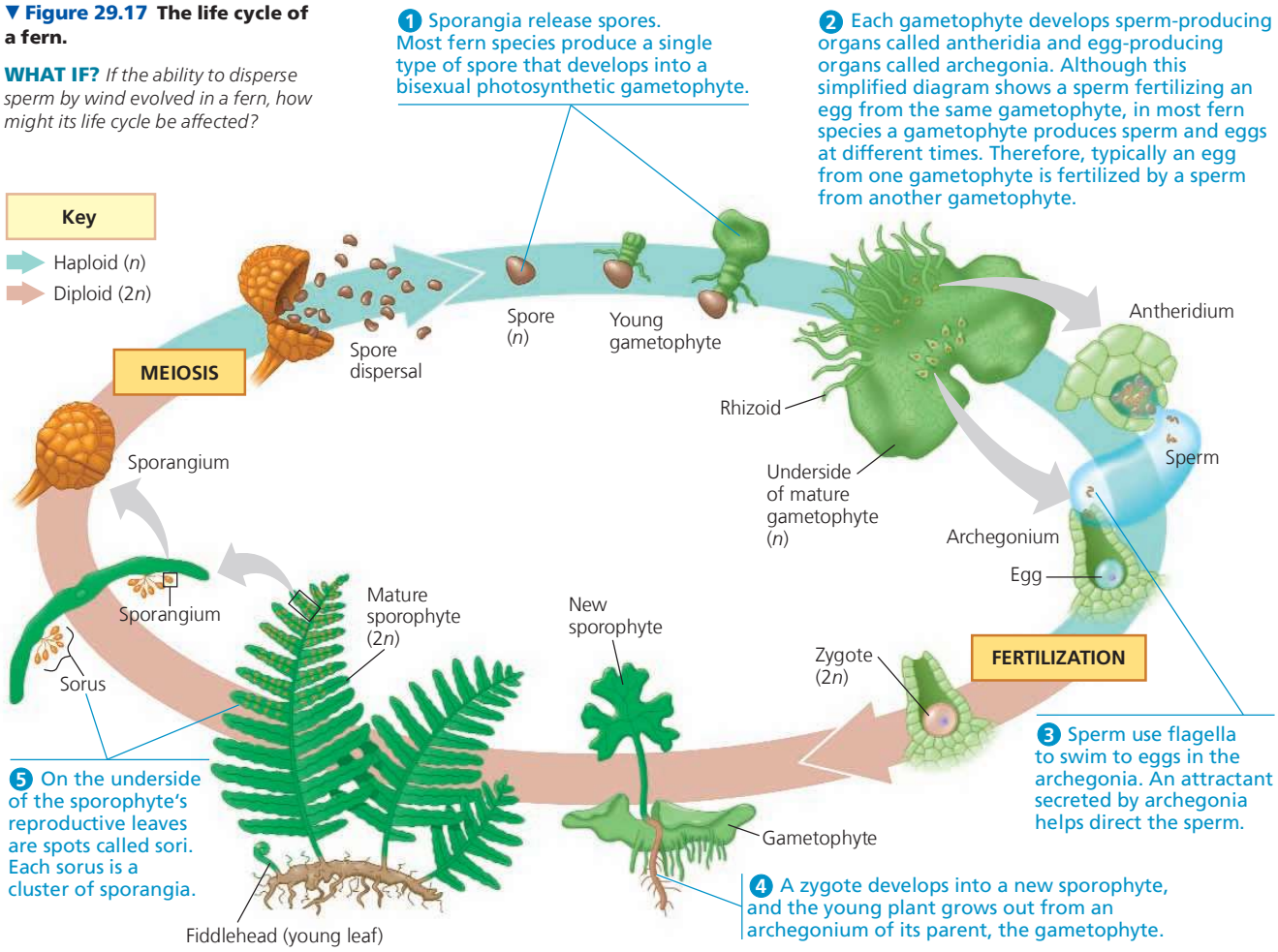
As mentioned earlier, mosses and other bryophytes have life cycles dominated by gametophytes (see Figure 29.11). Fossil evidence suggests that a change began to develop in some of the earliest vascular plants, whose gametophytes and sporophytes were about equal in size. Further reductions in gametophyte size occurred among extant vascular plants; in these groups, the sporophyte generation is the larger and more complex form in the alternation of generations **(Figure 29.17)**. In ferns, for example, the familiar leafy plants are the sporophytes. You would have to get down on your hands and knees and search the ground carefully to find fern gametophytes, which are tiny structures that often grow on or just below the soil surface.

Transport in Xylem and Phloem

Vascular plants have two types of vascular tissue: xylem and phloem (see Figure 35.10). **Xylem** conducts most of the water and minerals. The xylem of all vascular plants includes **tracheids**, tube-shaped cells that carry water and minerals up from the roots. The water-conducting cells of the xylem are dead at functional maturity and are *lignified*; that is, their cell walls are strengthened by the polymer **lignin**. The tissue called **phloem** has cells arranged into tubes that distribute sugars, amino acids, and other organic products; these cells are alive at functional maturity.

▼ Figure 29.17 The life cycle of a fern.

WHAT IF? *If the ability to disperse sperm by wind evolved in a fern, how might its life cycle be affected?*



Mastering Biology **Animation: Fern Life Cycle**

Lignified vascular tissue helped enable vascular plants to grow tall. Their stems became strong enough to provide support against gravity, and they could transport water and mineral nutrients high above the ground. Tall plants could also outcompete short plants for access to the sunlight needed for photosynthesis. In addition, the spores of tall plants could disperse farther than those of short plants, enabling tall species to colonize new environments more rapidly. Overall, the ability to grow tall gave vascular plants a competitive edge over nonvascular plants, which typically are less than 5 cm in height. Over time, competition among vascular plants also would have increased, leading to selection for taller growth forms—a process that eventually gave rise to the trees that formed the first forests 385 million years ago.

Evolution of Roots

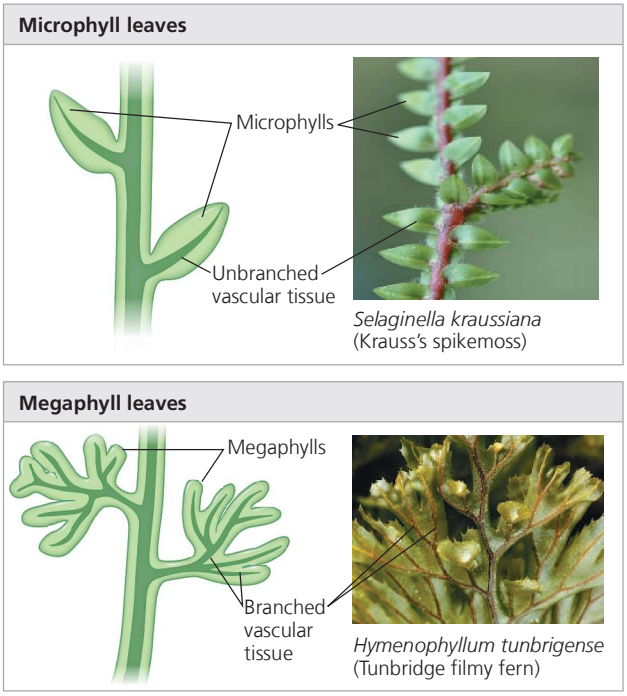
Vascular tissue also provides benefits below ground. Instead of the rhizoids seen in bryophytes, roots evolved in the sporophytes of almost all vascular plants. **Roots** are organs that absorb water and nutrients from the soil. Roots also anchor vascular plants to the ground, hence allowing the shoot system to grow taller.

Root tissues of living plants closely resemble stem tissues of early vascular plants preserved in fossils. This suggests that roots may have evolved from the lowest belowground portions of stems in ancient vascular plants. It is unclear whether roots evolved only once in the common ancestor of all vascular plants or independently in different lineages. Although the roots of living members of these lineages of vascular plants share many similarities, fossil evidence hints at convergent evolution. The oldest fossils of lycophytes, for example, already displayed simple roots 400 million years ago, when the ancestors of ferns and seed plants still had none. Studying genes that control root development in different vascular plant species may help resolve this question.

Evolution of Leaves

Leaves are structures that serve as the primary photosynthetic organ of vascular plants. In terms of size and

▼ **Figure 29.18** **Microphyll and megaphyll leaves.**



complexity, leaves can be classified as either microphylls or megaphylls **(Figure 29.18)**. All of the lycophytes—and only the lycophytes—have **microphylls**, which are small, often spine-shaped leaves supported by a single strand of vascular tissue. Almost all other vascular plants have **megaphylls**, leaves with a highly branched vascular system; a few species have reduced leaves that appear to have evolved from megaphylls. Megaphylls are typically larger than microphylls and therefore support greater photosynthetic productivity than microphylls. Microphylls first appear in the fossil record 410 million years ago, but megaphylls do not emerge until 370 million years ago, toward the end of the Devonian period.

Sporophylls and Spore Variations

One milestone in the evolution of plants was the emergence of **sporophylls**, modified leaves that bear sporangia. Sporophylls vary greatly in structure. For example, fern sporophylls produce clusters of sporangia known as **sori** (singular, *sorus*), usually on the undersides of the sporophylls (see Figure 29.17). In many lycophytes and in most gymnosperms, groups of sporophylls form cone-like structures called **strobili** (singular, *strobilus*). The sporophylls of angiosperms are called *carpels* and *stamens* (see Figure 30.8).

Most seedless vascular plant species are **homosporous**: They have one type of sporophyll bearing one type of sporangium that produces one type of spore, which typically develops into a bisexual gametophyte, as in most ferns. In contrast, a **heterosporous** species has two types of sporophylls, called megasporophylls and microsporophylls. Megasporophylls have megasporangia, which produce **megaspores**, spores that develop into female gametophytes. Microsporophylls have microsporangia, which produce **microspores**, smaller spores that develop into male gametophytes. All seed plants and a few seedless vascular plants are heterosporous. The following diagram compares the two conditions:

Homosporous spore production
(most seedless vascular plants)

Sporangium on sporophyll → Single type of spore → Typically a bisexual gametophyte → Eggs, Sperm

Heterosporous spore production
(all seed plants)

Megasporangium on megasporophyll → Megaspore → Female gametophyte → Eggs

Microsporangium on microsporophyll → Microspore → Male gametophyte → Sperm

Classification of Seedless Vascular Plants

As we noted earlier, biologists recognize two clades of living seedless vascular plants: the lycophytes (phylum Lycophyta) and the monilophytes (phylum Monilophyta). The lycophytes include the club mosses, the spikemosses, and the quillworts. The monilophytes include the ferns, the horsetails, and the whisk ferns and their relatives. Although ferns, horsetails, and whisk ferns differ greatly in appearance, recent anatomical and molecular comparisons provide convincing evidence that these three groups make up a clade. Accordingly, many systematists now classify them together as the phylum Monilophyta, as we do in this chapter. Others refer to these groups as three separate phyla within a clade. **Figure 29.19** describes the two main groups of seedless vascular plants.

Phylum Lycophyta: Club Mosses, Spikemosses, and Quillworts

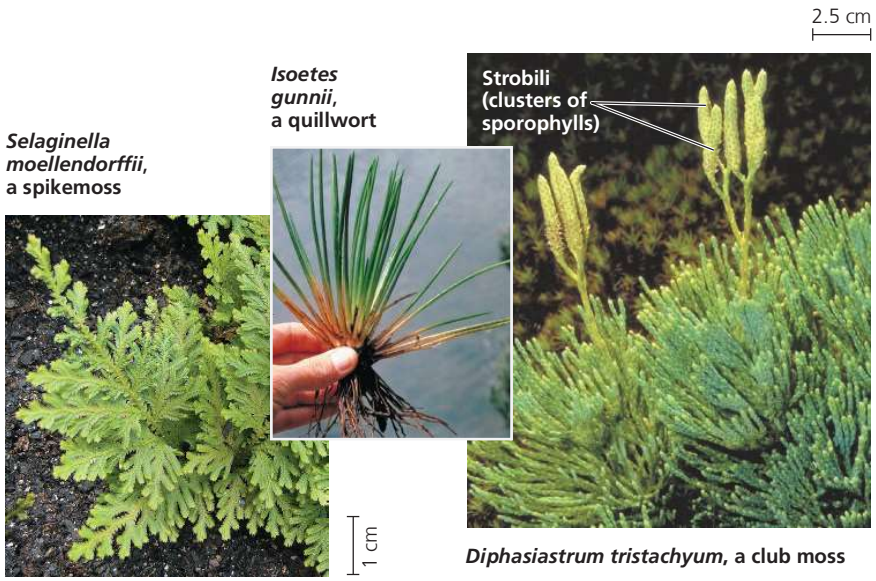
Present-day species of lycophytes are relicts of a far more impressive past. By the Carboniferous period (359–299 million years ago), the lycophyte evolutionary lineage included small herbaceous plants and giant trees with diameters of more than 2 m and heights of more than 40 m. The giant lycophyte trees thrived for millions of years in moist swamps, but their diversity declined when Earth's climate became drier during the Permian period (299–252 million years ago). The small lycophytes survived, represented today by about 1,200 species. Though some are commonly called club mosses and spikemosses, they are not true mosses (which, as discussed earlier, are nonvascular plants).

▼ Figure 29.19 Exploring Seedless Vascular Plant Diversity

Lycophytes (Phylum Lycophyta)

Many lycophytes grow on tropical trees as epiphytes, plants that use other plants as a substrate but are not parasites. Other species grow on temperate forest floors. In some species, the tiny gametophytes live above ground and are photosynthetic. Others live below ground, nurtured by symbiotic fungi.

Sporophytes have upright stems with many small leaves, as well as ground-hugging stems that produce dichotomously branching roots. Spikemosses are usually relatively small and often grow horizontally. In many club mosses and spikemosses, sporophylls are clustered into club-shaped cones (strobili). Quillworts, named for their leaf shape, form a single genus whose members live in marshy areas or as submerged aquatic plants. Club mosses are all homosporous, whereas spikemosses and quillworts are all heterosporous. The spores of club mosses are released in clouds and are so rich in oil that magicians and photographers once ignited them to create smoke or flashes of light.



Diphasiastrum tristachyum, a club moss

Monilophytes (Phylum Monilophyta)



Matteuccia struthiopteris (ostrich fern)

Ferns

Unlike the lycophytes, ferns have megaphylls (see Figure 29.18). The sporophytes typically have horizontal stems that give rise to large leaves called fronds, often divided into leaflets. A frond grows as its coiled tip, the fiddlehead, unfurls.

Almost all species are homosporous. The gametophyte in some species shrivels and dies after the young sporophyte detaches itself. In most species, sporophytes have stalked sporangia with springlike devices that catapult spores several meters. Airborne spores can be carried far from their origin. Some species produce more than a trillion spores in a plant's lifetime.



Equisetum telmateia, giant horsetail

Horsetails

The group's name refers to the brushy appearance of the stems, which have a gritty texture that made them historically useful as "scouring rushes" for pots and pans. Some species have separate fertile (cone-bearing) and vegetative stems. Horsetails are homosporous, with cones releasing spores that typically give rise to bisexual gametophytes.

Horsetails are also called arthrophytes ("jointed plants") because their stems have joints. Rings of small leaves or branches emerge from each joint, but the stem is the main photosynthetic organ. Large air canals carry oxygen to the roots, which often grow in waterlogged soil.



Psilotum nudum, a whisk fern

Whisk Ferns and Relatives

Like primitive vascular plant fossils, the sporophytes of whisk ferns (genus *Psilotum*) have dichotomously branching stems but no roots. Stems have scalelike outgrowths that lack vascular tissue and may have resulted from the evolutionary reduction of leaves. Each yellow knob on a stem consists of three fused sporangia. Species of the genus *Tmesipteris* closely related to whisk ferns and found only in the South Pacific, also lack roots but have small, leaflike outgrowths in their stems, giving them a vine-like appearance. Both genera are homosporous, with spores giving rise to bisexual gametophytes that grow underground and are only about a centimeter long.

Phylum Monilophyta: Ferns, Horsetails, and Whisk Ferns and Relatives

Ferns radiated extensively from their Devonian origins and grew alongside lycophyte trees and horsetails in the great Carboniferous swamp forests. Today, ferns are by far the most widespread seedless vascular plants, numbering more than 12,000 species. Though most diverse in the tropics, many ferns thrive in temperate forests, and some species are even adapted to arid habitats.

As mentioned earlier, ferns and other monilophytes are more closely related to seed plants than to lycophytes. As a result, monilophytes and seed plants share traits that are not found in lycophytes, including megaphyll leaves and roots that can branch at various points along the length of an existing root. In lycophytes, by contrast, roots branch only at the growing tip of the root, forming a Y-shaped structure.

The monilophytes called horsetails were very diverse during the Carboniferous period, some growing as tall as 15 m. Today, only 15 species survive as a single, widely distributed genus, *Equisetum*, often found in marshy places and along streams.

Psilotum (whisk ferns) and a closely related genus, *Tmesipteris*, form a clade consisting mainly of tropical epiphytes. Plants in these two genera, the only vascular plants lacking true roots, once were called "living fossils" because of their resemblance to fossils of ancient relatives of living vascular plants (see Figures 29.16 and 29.19). However, much evidence, including analyses of DNA sequences and sperm structure, indicates that the genera *Psilotum* and *Tmesipteris* are closely related to ferns. This hypothesis suggests that their ancestor's true roots were lost during evolution. Today, plants in these two genera absorb water and nutrients through numerous absorptive rhizoids.

The Significance of Seedless Vascular Plants

The ancestors of living lycophytes, horsetails, and ferns, along with their extinct seedless vascular relatives, grew to great heights during the Devonian and early Carboniferous, forming the first forests **(Figure 29.20)**. How did their dramatic growth affect Earth and its other life?

One major effect was that early forests contributed to a large drop in CO_2 levels during the Carboniferous period, causing global cooling that resulted in widespread glacier formation. The trees of early forests contributed to this drop in CO_2 levels in part by the actions of their roots. The roots of vascular plants secrete acids that break down rocks, thereby increasing the rate at which calcium and magnesium are released from rocks into the soil. These chemicals react with carbon dioxide dissolved in rain water, forming compounds that ultimately wash into the oceans, where they are incorporated into rocks (calcium or magnesium carbonates). The net effect of these processes—which were accelerated by plants—is that CO_2 removed from the air is stored in marine rocks. Although carbon stored in these rocks can be returned to the atmosphere, it typically takes millions of years for this to occur (as when geological uplift brings the rocks to the surface, exposing them to erosion).

In addition, the seedless vascular plants that formed the first forests eventually became coal, again removing CO_2 from the atmosphere for long periods of time. In the stagnant waters of Carboniferous swamps, the dead bodies of early trees did not completely decay. This organic material turned to thick layers of peat, later covered by the sea. Marine sediments piled on top, and over millions of years, heat and pressure converted the peat to coal. In fact, Carboniferous coal deposits are the most extensive ever formed. Coal was crucial to the Industrial Revolution, and people worldwide still burn 6 billion tons a year. It is ironic that coal, formed from plants that contributed to



▶ Figure 29.20 Artist's conception of a Carboniferous forest based on fossil evidence. Lycophyte trees, with trunks covered with small leaves, thrived in the "coal forests" of the Carboniferous, along with giant ferns and horsetails.

a global cooling, now contributes to global warming by returning carbon to the atmosphere (see Figure 56.29).

Growing along with the seedless plants in Carboniferous swamps were primitive seed plants. Though seed plants were not dominant at that time, they rose to prominence after the swamps began to dry up at the end of the Carboniferous period. The next chapter traces the origin and diversification of seed plants, continuing our story of adaptation to life on land.

CONCEPT CHECK 29.3

1. List the key derived traits found in monilophytes and seed plants, but not in lycophytes.
2. How do the main similarities and differences between seedless vascular plants and nonvascular plants affect function in these plants?
3. **MAKE CONNECTIONS** In Figure 29.17, if fertilization occurred between gametes from one gametophyte, how would this affect the production of genetic variation from sexual reproduction? See Concept 13.4.

For suggested answers, see Appendix A.

29 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

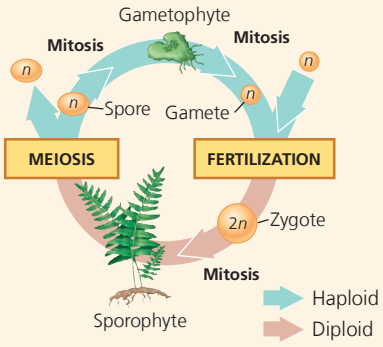
SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

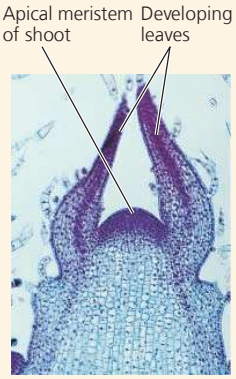
CONCEPT 29.1

Plants evolved from green algae *(pp. 619–623)*

- Morphological and biochemical traits, as well as similarities in nuclear and chloroplast genes, indicate that certain charophyte algae are the closest living relatives of plants.
- A protective layer of **sporopollenin** and other traits allow charophytes to tolerate occasional drying along the edges of ponds and lakes. Such traits may have enabled the algal ancestors of plants to survive in terrestrial conditions, opening the way to the colonization of dry land.
- Derived traits that distinguish plants from charophytes, their closest algal relatives, include **cuticles, stomata,** multicellular dependent embryos, walled spores produced in sporangia, and the two shown here:



1 Alternation of generations



2 Apical meristems

- Fossils show that plants arose more than 470 million years ago. Subsequently, plants diverged into several major groups, including nonvascular plants (**bryophytes**); **seedless vascular plants**, such as **lycophytes** and ferns; and the two groups of seed plants: **gymnosperms** and **angiosperms**.

? *Draw a phylogenetic tree illustrating our current understanding of plant phylogeny; label the common ancestor of plants and the origins of vascular tissue, apical meristems, and seeds.*

CONCEPT 29.2

Mosses and other nonvascular plants have life cycles dominated by gametophytes *(pp. 623–629)*

- Lineages leading to the three extant clades of nonvascular plants, or **bryophytes—liverworts, mosses**, and **hornworts**—diverged from other plants early in plant evolution.
- In bryophytes, the dominant generation consists of haploid **gametophytes**, such as those that make up a carpet of moss. **Rhizoids** anchor gametophytes to the substrate on which they grow. The flagellated sperm produced by **antheridia** require a film of water to travel to the eggs in the **archegonia**.
- The diploid stage of the life cycle—the **sporophytes**—grow out of archegonia and are attached to the gametophytes and dependent on them for nourishment. Smaller and simpler than vascular plant sporophytes, they typically consist of a **foot, seta** (stalk), and **sporangium**.
- *Sphagnum*, or peat moss, is common in large regions known as peatlands and has many practical uses, including as a fuel.

? *Summarize the ecological importance of mosses.*

CONCEPT 29.3

Ferns and other seedless vascular plants were the first plants to grow tall *(pp. 629–634)*

- Fossils of the forerunners of today's vascular plants date back about 425 million years and show that these small plants had independent, branching sporophytes and a vascular system.
- Over time, other derived traits of living vascular plants arose, such as a life cycle with dominant sporophytes, lignified vascular tissue, well-developed **roots** and **leaves**, and **sporophylls**.
- Seedless vascular plants include the **lycophytes** (phylum Lycophyta: club mosses, spikemosses, and quillworts) and the **monilophytes** (phylum Monilophyta: ferns, horsetails, and whisk ferns and relatives). Current evidence indicates that seedless vascular plants, like bryophytes, do not form a clade.
- Ancient lineages of lycophytes included both small herbaceous plants and large trees. Present-day lycophytes are small herbaceous plants.
- Seedless vascular plants formed the earliest forests 385 million years ago. Their growth may have contributed to a major global cooling that took place during the Carboniferous period. The decaying remnants of the first forests eventually became coal.

? *What trait(s) allowed vascular plants to grow tall, and why might increased height have been advantageous?*

TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

1. Three of the following are evidence that charophytes are the closest algal relatives of plants. Select the exception.
   (A) similar sperm structure
   (B) the presence of chloroplasts
   (C) similarities in cell wall formation during cell division
   (D) genetic similarities in chloroplasts
2. Which of the following characteristics of plants is absent in their closest relatives, the charophyte algae?
   (A) chlorophyll *b*
   (B) cellulose in cell walls
   (C) sexual reproduction
   (D) alternation of multicellular generations
3. In plants, which of the following are produced by meiosis?
   (A) haploid gametes
   (B) diploid gametes
   (C) haploid spores
   (D) diploid spores
4. Microphylls are found in which plant group?
   (A) lycophytes
   (B) liverworts
   (C) ferns
   (D) hornworts

Levels 3-4: Applying/Analyzing

5. Suppose an efficient conducting system evolved in a moss that could transport water and other materials as high as a tall tree. Which of the following statements about "trees" of such a species would be true?
   (A) Spore dispersal distances would probably decrease.
   (B) Females could produce only one archegonium.
   (C) Unless its body parts were strengthened, such a "tree" would probably flop over.
   (D) Individuals would probably compete less effectively for access to light.
6. Identify each of the following structures as haploid or diploid.
   a. sporophyte
   b. spore
   c. gametophyte
   d. zygote
7. **EVOLUTION CONNECTION • DRAW IT** Draw a phylogenetic tree that represents our current understanding of evolutionary relationships between a moss, a gymnosperm, a lycophyte, and a fern. Use a charophyte alga as the outgroup. (See Figure 26.5 to review phylogenetic trees.) Label each branch point of the phylogeny with at least one derived character unique to the clade descended from the common ancestor represented by the branch point.

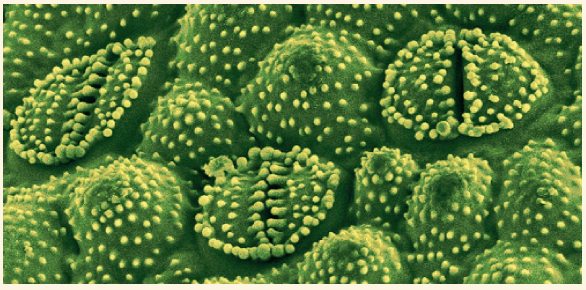
Levels 5-6: Evaluating/Creating

8. **SCIENTIFIC INQUIRY • INTERPRET THE DATA** The feather moss *Pleurozium schreberi* harbors species of symbiotic nitrogen-fixing bacteria. Scientists studying this moss in northern forests found that the percentage of the ground surface "covered" by the moss increased from about 5% in forests that burned 35 to 41 years ago to about 70% in forests that burned 170 or more years ago. From mosses growing in these forests, they also obtained the following data on nitrogen fixation:

Age (years after fire)	N fixation rate [kg N/(ha · yr)]
35	0.001
41	0.005
78	0.08
101	0.3
124	0.9
170	2.0
220	1.3
244	2.1
270	1.6
300	3.0
355	2.3

Data from O. Zackrisson et al., Nitrogen fixation increases with successional age in boreal forests, *Ecology* 85:3327–3334 (2006).

   (a) Use the data to draw a line graph, with age on the *x*-axis and the nitrogen fixation rate on the *y*-axis.
   (b) Along with the nitrogen added by nitrogen fixation, about 1 kg of nitrogen per hectare per year is deposited into northern forests from the atmosphere as rain and small particles. Evaluate the extent to which *Pleurozium* affects nitrogen availability in northern forests of different ages.
9. **WRITE ABOUT A THEME: INTERACTIONS** Giant lycophyte trees had microphylls, whereas ferns and seed plants have megaphylls. Write a short essay (100–150 words) describing how a forest of lycophyte trees may have differed from a forest of large ferns or seed plants. In your answer, consider how the type of forest may have affected interactions among small plants growing beneath the tall ones.
10. **SYNTHESIZE YOUR KNOWLEDGE**



These stomata are from the leaf of a common horsetail. Describe how stomata and other adaptations facilitated life on land and ultimately led to the formation of the first forests.

For selected answers, see Appendix A.

30 Plant Diversity II: The Evolution of Seed Plants

KEY CONCEPTS

30.1 **Seeds and pollen grains are key adaptations for life on land** *p. 637*

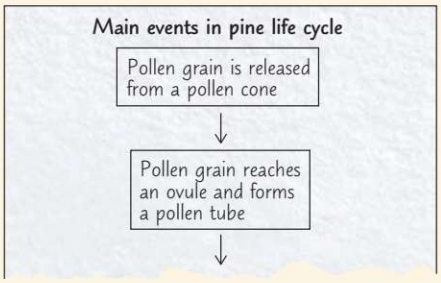
30.2 **Gymnosperms bear "naked" seeds, typically on cones** *p. 640*

30.3 **The reproductive adaptations of angiosperms include flowers and fruits** *p. 644*

30.4 **Human welfare depends on seed plants** *p. 651*

Study Tip

Make flowcharts: Make simple flowcharts showing the main events in the life cycles of a pine and flowering plant. The example shown is the beginning of a flowchart summarizing the pine life cycle.



Go to Mastering Biology

For Students (in eText and Study Area)
- Get Ready for Chapter 30
- Figure 30.3 Walkthrough: From Ovule to Seed in a Gymnosperm
- Figure 30.12 Walkthrough: The Life Cycle of an Angiosperm
- Animation: Angiosperm Life Cycle

For Instructors to Assign (in Item Library)
- Scientific Skills Exercise: Using Natural Logarithms to Interpret Data
- Tutorial: Gymnosperms



Figure 30.1 In 1980, Mount St. Helens in Washington state erupted, leaving the region covered in ash and devoid of visible life. Just a few years later, seed plants such as fireweed (*Chamerion angustifolium*) had already colonized the barren landscape—an example of seed plants' versatility and success as the dominant producers on land.



Fireweed seed

What adaptations have enabled seed plants to make up the vast majority of plant biodiversity?

Reduced male and female gametophytes develop within parental sporophytes, protected from environmental stresses.

In **gymnosperms,** the gametophytes develop within cones.



In **angiosperms,** the gametophytes develop within flowers.

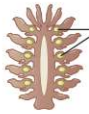


Pollen protects male gametophytes (which produce sperm) and can be transported by wind or animals.



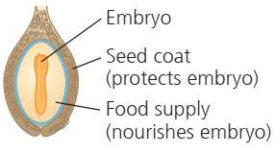


Ovules protect female gametophytes (which produce eggs).





An ovule fertilized by pollen develops into a **seed**.



Fireweed and other early arrivals reached the blast zone in Figure 30.1 as seeds. A **seed** consists of an embryo and its food supply, surrounded by a protective coat. When mature, seeds are dispersed from their parent by wind or other means, enabling them to colonize distant locations.

Plants not only have affected the recovery of regions such as Mount St. Helens but also have transformed Earth. Continuing the saga of how this occurred, this chapter follows the emergence and diversification of the group to which fireweed belongs, the seed plants.

CONCEPT 30.1

Seeds and pollen grains are key adaptations for life on land

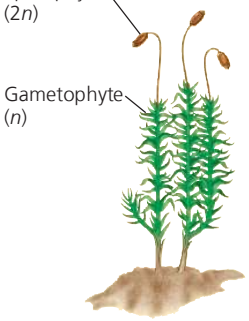
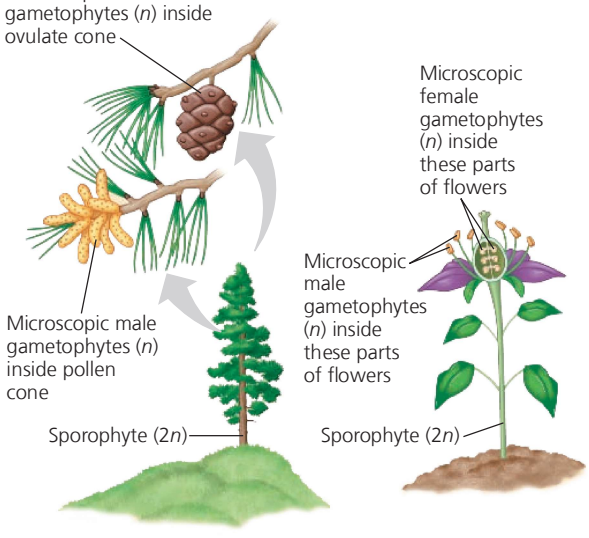
We begin with an overview of terrestrial adaptations that seed plants added to those already present in nonvascular plants (bryophytes) and seedless vascular plants (see Concept 29.1). In addition to seeds, all seed plants have reduced gametophytes, heterospory, ovules, and pollen. As we'll see, these adaptations helped seed plants cope with conditions such as drought and exposure to ultraviolet (UV) radiation in sunlight. They also freed seed plants from requiring water for fertilization, enabling reproduction under a broader range of conditions than in seedless plants.

Advantages of Reduced Gametophytes

Mosses and other bryophytes have life cycles dominated by gametophytes, whereas ferns and other seedless vascular plants have sporophyte-dominated life cycles. The evolutionary trend of gametophyte reduction continued further in the vascular plant lineage that led to seed plants **(Figure 30.2)**. While the gametophytes of seedless vascular plants are visible to the naked eye, the gametophytes of most seed plants are microscopic.

This miniaturization allowed for an important evolutionary innovation in seed plants: Their tiny gametophytes can develop from spores retained within the sporangia of the parental sporophyte. This arrangement can protect the gametophytes from environmental stresses. For example, the moist reproductive tissues of the sporophyte shield the gametophytes from UV radiation and protect them from drying out. This relationship

▼ Figure 30.2 Gametophyte-sporophyte relationships in different plant groups.

	PLANT GROUP		
	Mosses and other nonvascular plants	**Ferns and other seedless vascular plants**	**Seed plants (gymnosperms and angiosperms)**
Gametophyte	Dominant	Reduced, independent (photosynthetic and free-living)	Reduced (usually microscopic), dependent on surrounding sporophyte tissue for nutrition
Sporophyte	Reduced, dependent on gametophyte for nutrition	Dominant	Dominant
Example			**Gymnosperm** **Angiosperm** 

MAKE CONNECTIONS *In seed plants, how might retaining the gametophyte within the sporophyte affect embryo fitness? (See Concepts 17.5, 23.1, and 23.4 to review mutagens, mutations, and fitness.)*

also enables the developing gametophytes to obtain nutrients from the parental sporophyte. In contrast, the free-living gametophytes of seedless vascular plants must fend for themselves.

Heterospory: The Rule Among Seed Plants

You read in Concept 29.3 that most seedless plants are *homosporous*—they produce one kind of spore, which usually gives rise to a bisexual gametophyte. Ferns and other close relatives of seed plants are homosporous, suggesting that seed plants had homosporous ancestors. At some point, seed plants or their ancestors became *heterosporous*, producing two kinds of spores: Megasporangia on modified leaves called megasporophylls produce *megaspores* that give rise to female gametophytes, and microsporangia on modified leaves called microsporophylls produce *microspores* that give rise to male gametophytes. Each megasporangium has one megaspore, whereas each microsporangium has many microspores.

As noted previously, the miniaturization of seed plant gametophytes probably contributed to the great success of this clade. Next, we'll look at the development of the female gametophyte within an ovule and the development of the male gametophyte in a pollen grain. Then we'll follow the transformation of a fertilized ovule into a seed.

Ovules and Production of Eggs

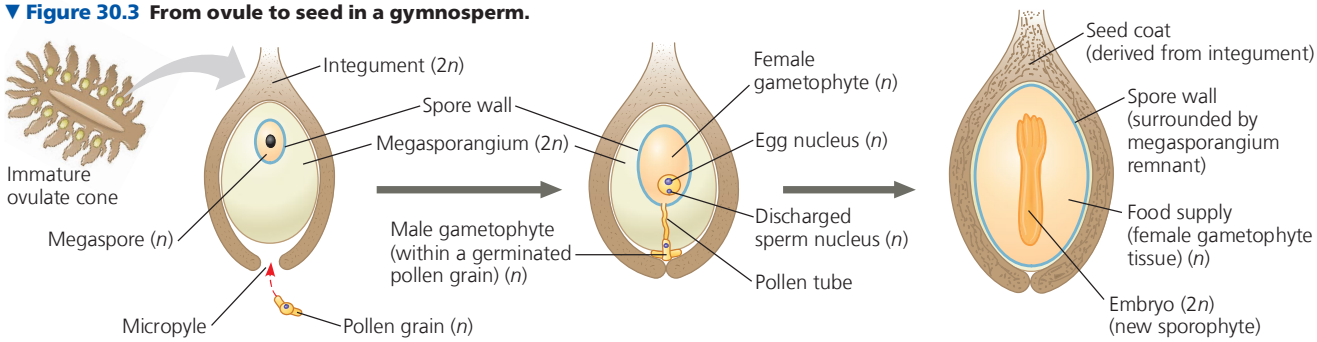
Although a few species of seedless plants are heterosporous, seed plants are unique in retaining the megasporangium within the parent sporophyte. A layer of sporophyte tissue called **integument** envelops and protects the megasporangium. Gymnosperm megasporangia are surrounded by one integument, whereas those in angiosperms usually have two integuments. The whole structure—megasporangium, megaspore, and their integument(s)—is called an **ovule (Figure 30.3a)**. Inside each ovule (from the Latin *ovulum*, little egg), a female gametophyte develops from a megaspore and produces one or more eggs.

Pollen and Production of Sperm

A microspore develops into a **pollen grain** that consists of a male gametophyte enclosed within the pollen wall. (The wall's outer layer is made of molecules secreted by sporophyte cells, so we refer to the male gametophyte as being *in* the pollen grain, not *equivalent to* the pollen grain.) Sporopollenin in the pollen wall protects the pollen grain as it is transported by wind or by hitchhiking on an animal. The transfer of pollen to the part of a seed plant that contains the ovules is called **pollination**. If a pollen grain germinates (begins growing), it gives rise to a pollen tube that discharges sperm into the female gametophyte within the ovule, as shown in **Figure 30.3b**.

In nonvascular plants and seedless vascular plants such as ferns, free-living gametophytes release flagellated sperm that swim through a film of water to reach eggs. Given this requirement, it is not surprising that many of these species live in moist habitats. But a pollen grain can be carried by wind or animals, eliminating the dependence on water for sperm transport. The ability of seed plants to transfer sperm without water likely contributed to their colonization of dry habitats. The sperm of seed plants also do not require motility because they are carried to the eggs by pollen tubes. The sperm of some gymnosperm species (such as cycads and ginkgos, shown in Figure 30.7) retain the ancient flagellated condition, but flagella have been lost in the sperm of most gymnosperms and all angiosperms.

▼ Figure 30.3 From ovule to seed in a gymnosperm.



(a) Unfertilized ovule. In this longitudinal section through the ovule of a pine (a gymnosperm), a fleshy megasporangium is surrounded by a protective layer of tissue called an integument. The micropyle, the only opening through the integument, allows entry of a pollen grain.

(b) Fertilized ovule. A megaspore develops into a female gametophyte, which produces an egg. The pollen grain, which had entered through the micropyle, contains a male gametophyte. The male gametophyte develops a pollen tube that discharges sperm, thereby fertilizing the egg.

(c) Gymnosperm seed. Fertilization initiates the transformation of the ovule into a seed, which consists of a sporophyte embryo, a food supply, and a protective seed coat derived from the integument. The megasporangium dries out and collapses.

VISUAL SKILLS *Based on this figure, a gymnosperm seed contains cells from how many different plant generations? Identify the cells and whether each is haploid or diploid.*

Mastering Biology Figure Walkthrough

Scientific Skills Exercise

Using Natural Logarithms to Interpret Data

How Long Can Seeds Remain Viable in Dormancy? Environmental conditions can vary greatly over time, and they may not be favorable for germination when seeds are produced. One way that plants cope with such variation is through seed dormancy. Under favorable conditions, seeds of some species can germinate after many years of dormancy.

One unusual opportunity to test how long seeds can remain viable occurred when seeds from date palm trees (*Phoenix dactylifera*) were discovered under the rubble of a 2,000-year-old fortress near the Dead Sea. As you saw in the Chapter 2 Scientific Skills Exercise and Concept 25.2, scientists use radiometric dating to estimate the ages of fossils and other old objects. In this exercise, you will estimate the ages of three of these ancient seeds by using natural logarithms.

How the Experiment Was Done Scientists measured the fraction of carbon-14 that remained in three ancient date palm seeds: two that were not planted and one that was planted and germinated. For the germinated seed, the scientists used a seed coat fragment found clinging to a root of the seedling. (The seedling grew into the plant in the photo.)

Data from the Experiment This table shows the fraction of carbon-14 remaining from the three ancient date palm seeds.

	Fraction of Carbon-14 Remaining
Seed 1 (not planted)	0.7656
Seed 2 (not planted)	0.7752
Seed 3 (germinated)	0.7977



INTERPRET THE DATA

A logarithm is the power to which a base is raised to produce a given number x. For example, if the base is 10 and $x = 100$, the logarithm of 100 equals 2 (because $10^2 = 100$). A natural logarithm (ln) is the logarithm of a number x to the base e, where e is about 2.718. Natural logarithms are useful in calculating rates of some natural processes, such as radioactive decay.

The equation $F = e^{-kt}$ describes the fraction F of an original isotope remaining after a period of t years; the exponent is negative because it refers to a *decrease* over time. The constant k provides a measure of how rapidly the original isotope decays. For the decay of carbon-14 to nitrogen-14, $k = 0.00012097$.

To estimate t, the age of the three seeds, we rearrange the equation $F = e^{-kt}$ to find an equation for t:

$$t = -\left(\frac{\ln F}{k}\right)$$

1. Using the equation for t, the data from the table, and a calculator, estimate the ages of seed 1, seed 2, and seed 3.
2. Why do you think there was more carbon-14 in the germinated seed?

Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

Data from S. Sallon et al., Germination, genetics, and growth of an ancient date seed, *Science* 320:1464 (2008).

The Evolutionary Advantage of Seeds

If a sperm fertilizes an egg of a seed plant, the zygote grows into a sporophyte embryo. As shown in **Figure 30.3c**, the ovule develops into a seed: the embryo, with a food supply, packaged in a protective coat derived from the integument(s).

Seeds provide protection from harsh conditions and facilitate dispersal to new habitats—as do the spores of seedless plants. Moss spores, for example, may survive even if the local environment becomes too cold, too hot, or too dry for the mosses themselves to live. Their tiny size enables the spores to be dispersed in a dormant state to a new area, where they can germinate and give rise to new moss gametophytes if and when conditions are favorable enough for them to break dormancy. Spores were the main way that mosses, ferns, and other seedless plants spread over Earth for the first 100 million years of plant life on land.

Although mosses and other seedless plants continue to be very successful today, seeds represent a major evolutionary innovation that contributed to the opening of new ways of life for seed plants. What advantages do seeds provide over spores? Spores are usually single-celled, whereas seeds are multicellular, consisting of an embryo protected by a layer of tissue, the seed coat. A seed can remain dormant for days, months, or even years after being released from the parent plant, whereas most spores have shorter lifetimes. Also, unlike spores, seeds have a supply of stored food. Most seeds land close to their parent sporophyte plant, but some are carried long distances (up to hundreds of kilometers) by wind or animals. If conditions are favorable where it lands, the seed can emerge from dormancy and germinate, with its stored food providing critical support for growth as the sporophyte embryo emerges as a seedling. As we explore in the **Scientific Skills Exercise**, some seeds have germinated after more than 1,000 years.

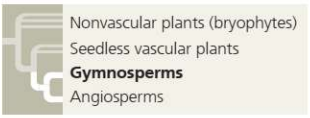
CONCEPT CHECK 30.1

1. Contrast how sperm reach the eggs of seedless plants with how sperm reach the eggs of seed plants.
2. What features not present in seedless plants have contributed to the success of seed plants on land?
3. **WHAT IF?** If a seed could not enter dormancy, how might that affect the embryo's transport or survival?

For suggested answers, see Appendix A.

CONCEPT 30.2

Gymnosperms bear "naked" seeds, typically on cones

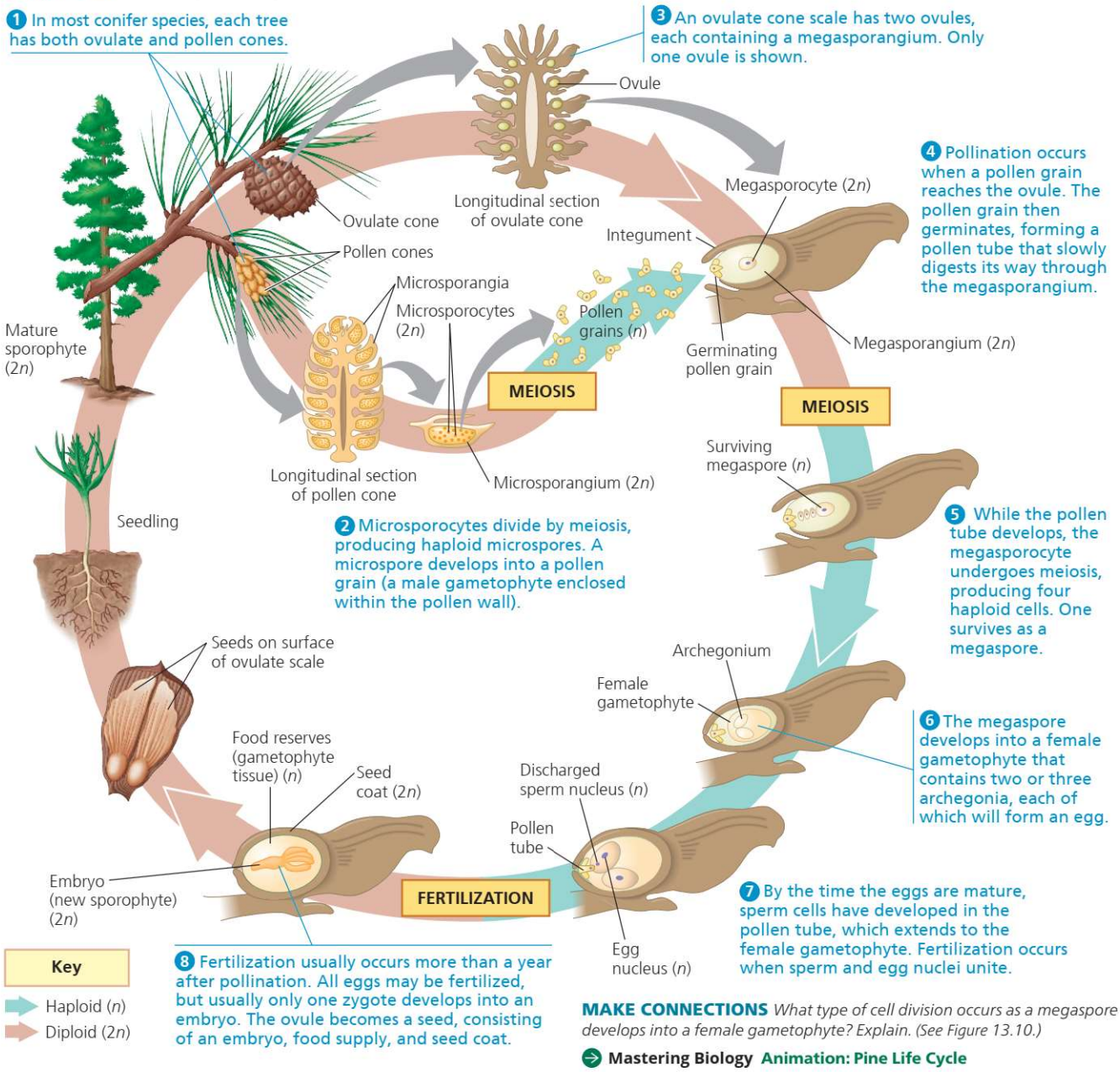


Extant seed plants form two sister clades: gymnosperms and angiosperms. Recall that gymnosperms have "naked" seeds exposed on sporophylls that usually form cones. (Angiosperm seeds are enclosed in chambers that mature into fruits.) Most gymnosperms are cone-bearing plants called **conifers**, such as pines, firs, and redwoods.

The Life Cycle of a Pine

As you read earlier, seed plant evolution has included three key reproductive adaptations: the miniaturization of their gametophytes; the advent of the seed as a resistant, dispersible stage in the life cycle; and the appearance of pollen as an airborne agent that brings gametes together. **Figure 30.4** shows how these adaptations come into play during the life cycle of a pine, a familiar conifer.

▼ Figure 30.4 The life cycle of a pine.



MAKE CONNECTIONS *What type of cell division occurs as a megaspore develops into a female gametophyte? Explain. (See Figure 13.10.)*

Mastering Biology **Animation: Pine Life Cycle**

The pine tree is the sporophyte; its sporangia are located on scalelike structures packed densely in cones. Like all seed plants, conifers are heterosporous. As such, they have two types of sporangia that produce two types of spores: microsporangia that produce microspores and megasporangia that produce megaspores. In conifers, the two types of spores are produced by separate cones: small pollen cones and large ovulate cones.

Pollen cones have a relatively simple structure: Their scales are modified leaves (microsporophylls) that bear microsporangia. Within each microsporangium, cells called microsporocytes undergo meiosis, producing haploid microspores. Each microspore develops into a pollen grain containing a male gametophyte. In conifers, the yellow pollen is released in large amounts and carried by the wind, dusting everything in its path.

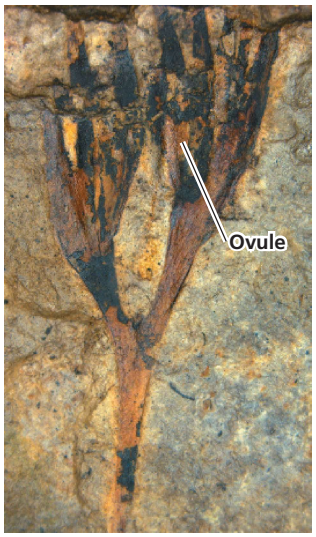
Ovulate cones are more complex: Their scales are compound structures composed of both modified leaves (megasporophylls bearing megasporangia) and modified stem tissue. Within each megasporangium, megasporocytes undergo meiosis and produce haploid megaspores inside the ovule. Surviving megaspores develop into female gametophytes, which are retained within the sporangia.

In most pine species, each tree has both types of cones. From the time pollen and ovulate cones appear on the tree, it takes nearly three years for the male and female gametophytes to be produced and brought together and for mature seeds to form from fertilized ovules. The scales of each ovulate cone then separate, and seeds are dispersed by the wind. A seed that lands in a suitable environment germinates, its embryo emerging as a pine seedling.

Early Seed Plants and the Rise of Gymnosperms

The origins of characteristics found in pines and other living seed plants date back to the late Devonian period (380 million years ago). Fossils from that time reveal that some plants had acquired features that are also present in seed plants, such as megaspores and microspores. For example, *Archaeopteris* was a heterosporous tree with a woody stem. It grew up to 20 m tall and had fernlike leaves. But it did not bear seeds and therefore is not classified as a seed plant.

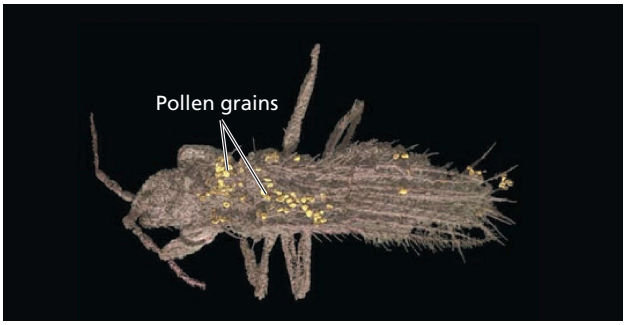
▼ Figure 30.5 A fossil of the early seed plant *Elkinsia*.



The earliest evidence of seed plants comes from 360-million-year-old fossils of plants in the genus *Elkinsia* **(Figure 30.5)**. These and other early seed plants lived 55 million years before the first fossils classified as gymnosperms and more than 200 million years before the first fossils of angiosperms. These early seed plants became extinct, and we don't know which extinct lineage gave rise to the gymnosperms.

The oldest fossils of species from an extant lineage of gymnosperms are 305 million years old. These early gymnosperms lived in moist Carboniferous ecosystems that were dominated by lycophytes, horsetails, ferns, and other seedless vascular plants. As the Carboniferous period gave way to the Permian (299 to 252 million years ago), the climate became much drier. As a result, the lycophytes, horsetails, and ferns that dominated Carboniferous swamps were largely replaced by gymnosperms, which were better suited to the drier climate.

▼ Figure 30.6 An ancient pollinator. This 110-million-year-old fossil shows pollen on an insect, the thrip *Gymnopollisthrips minor*. Structural features of the pollen suggest that it was produced by gymnosperms (most likely by species related to extant ginkgos or cycads). Although most gymnosperms today are wind-pollinated, many cycads are insect-pollinated.



Gymnosperms thrived as the climate dried, in part because they have the key terrestrial adaptations found in all seed plants, such as seeds and pollen. In addition, some gymnosperms were particularly well suited to arid conditions because of the thick cuticles and relatively small surface areas of their needle-shaped leaves.

Gymnosperms dominated terrestrial ecosystems throughout much of the Mesozoic era, which lasted from 252 to 66 million years ago. In addition to serving as the food supply for giant herbivorous dinosaurs, these gymnosperms were involved in many other interactions with animals. Recent fossil discoveries, for example, show that some gymnosperms were pollinated by insects more than 100 million years ago—the earliest evidence of insect pollination in any plant group **(Figure 30.6)**. Late in the Mesozoic, angiosperms began to replace gymnosperms in some ecosystems.

Gymnosperm Diversity

Although angiosperms now dominate most terrestrial ecosystems, gymnosperms remain an important part of Earth's flora. For example, vast regions in northern latitudes are covered by forests of conifers (see Figure 52.13).

Of the ten plant phyla (see Table 29.1), four are gymnosperms: Cycadophyta, Ginkgophyta, Gnetophyta, and Coniferophyta. It is uncertain how the four phyla of gymnosperms are related to each other. **Figure 30.7** surveys the diversity of extant gymnosperms.

▼ Figure 30.7 Exploring Gymnosperm Diversity

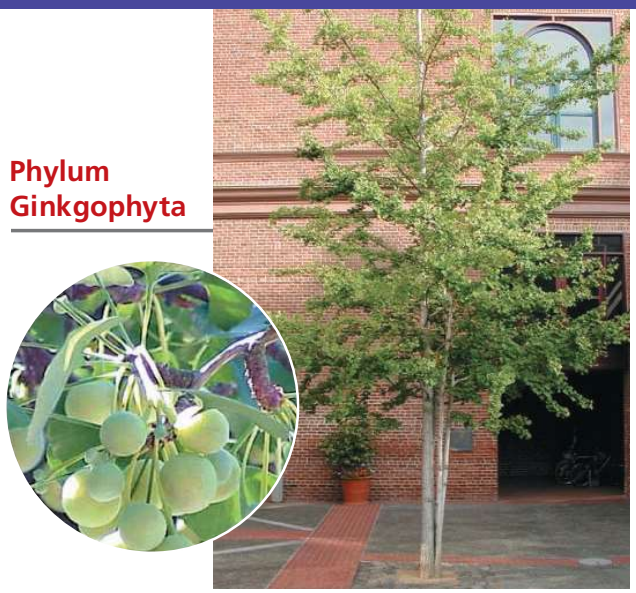
Phylum Cycadophyta

The 350 species of living cycads have large cones and palmlike leaves (true palm species are angiosperms). Unlike most seed plants, cycads have flagellated sperm, indicating their descent from seedless vascular plants that had motile sperm. Cycads thrived during the Mesozoic era, known as the age of cycads as well as the age of dinosaurs. Today, however, cycads are the most endangered of all plant groups: 75% of their species are threatened by habitat destruction and other human actions.



Cycas revoluta

Phylum Ginkgophyta



Ginkgo biloba is the only surviving species of this phylum; like cycads, ginkgos have flagellated sperm. Also known as the maidenhair tree, *Ginkgo biloba* has deciduous fanlike leaves that turn gold in autumn. It is a popular ornamental tree in cities because it tolerates air pollution well. Landscapers often plant only pollen-producing trees because the fleshy seeds smell rancid as they decay.

Phylum Gnetophyta

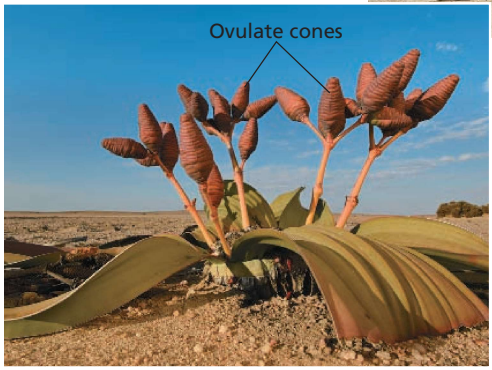
Phylum Gnetophyta includes plants in three genera: *Gnetum*, *Ephedra*, and *Welwitschia*. Some species are tropical, whereas others live in deserts. Although very different in appearance, the genera are grouped together based on molecular data.



◀ ***Gnetum.*** This genus includes about 35 species of tropical trees, shrubs, and vines, mainly native to Africa and Asia. Their leaves look similar to those of flowering plants, and their seeds look somewhat like fruits.

▶ ***Welwitschia*** (also below). This genus consists of one species, *Welwitschia mirabilis*, a plant that can live for thousands of years and is found only in the deserts of southwestern Africa. Its straplike leaves are among the largest leaves known.





▶ ***Ephedra.*** This genus includes about 40 species that inhabit arid regions worldwide. These desert shrubs, commonly called "Mormon tea," produce the compound ephedrine, which is used medicinally as a decongestant.



Phylum Coniferophyta

Phylum Coniferophyta, the largest gymnosperm phyla, consists of about 600 species of conifers (from the Latin *conus*, cone, and *ferre*, to carry), including many large trees. Most species have woody cones, but a few have fleshy cones. Some, such as pines, have needlelike leaves. Others, such as redwoods, have scalelike leaves. Some species dominate vast northern forests, whereas others are native to the Southern Hemisphere.

Most conifers are evergreens; they retain their leaves throughout the year. Even during winter, a limited amount of photosynthesis occurs on sunny days. When spring comes, conifers already have fully developed leaves that can take advantage of the sunnier, warmer days. Some conifers, such as the dawn redwood, tamarack, and larch, are deciduous trees that lose leaves each autumn.



▶ **Douglas fir.** This evergreen tree (*Pseudotsuga menziesii*) provides more timber than any other North American tree species. Some uses include house framing, plywood, pulpwood for paper, railroad ties, and boxes and crates.

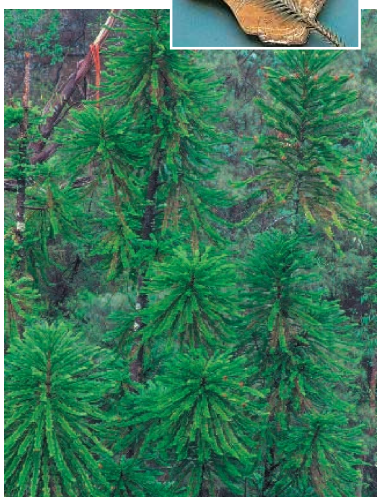


▶ **Common juniper.** The "berries" of the common juniper (*Juniperus communis*) are actually ovule-producing cones consisting of fleshy sporophylls.

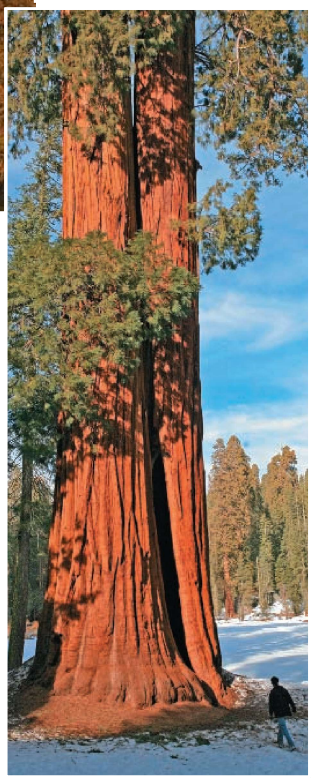


◀ **European larch.** The needlelike leaves of this deciduous conifer (*Larix decidua*) turn yellow before they are shed in autumn. Native to the mountains of central Europe, including Switzerland's Matterhorn, depicted here, this species is extremely cold-tolerant, able to survive winter temperatures that plunge to –50°C.





◀ **Wollemi pine.** Survivors of a conifer group once known only from fossils, living *Wollemi* pines (*Wollemia nobilis*) were discovered in 1994 in a national park near Sydney, Australia. At that time, the species consisted of 40 known trees. As a result of conservation efforts, it is now widely propagated. The inset photo compares the leaves of this "living fossil" with actual fossils.



▶ **Sequoia.** This giant sequoia (*Sequoiadendron giganteum*) in California's Sequoia National Park weighs about 2,500 metric tons, equivalent to about 24 blue whales (the largest animals) or 40,000 people. The giant sequoia is one of the largest living organisms and also among the most ancient, with some individuals estimated to be between 1,800 and 2,700 years old. Their cousins, the coast redwoods (*Sequoia sempervirens*), grow to heights of more than 110 m (taller than the Statue of Liberty) and are found only in a narrow coastal strip of northern California and southern Oregon.



▶ **Bristlecone pine.** This species (*Pinus longaeva*), which is found in the White Mountains of California, includes some of the world's oldest living organisms. One bristlecone pine was recently found to be more than 5,000 years old, and some may be even older.

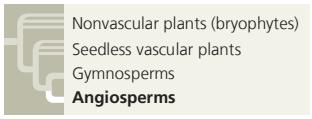
CONCEPT CHECK 30.2

1. Explain how the pine life cycle in Figure 30.4 reflects the five adaptations common to all seed plants.
2. **VISUAL SKILLS** Based on Figure 30.4, compare and contrast the function of pollination and fertilization in sexual reproduction in pines.
3. **MAKE CONNECTIONS** Early seed plants in genus *Elkinsia* are a sister group to a clade consisting of gymnosperms and angiosperms. Draw a phylogenetic tree of seed plants that shows *Elkinsia*, gymnosperms, and angiosperms; date the branch points on this tree using fossil evidence. (See Figure 26.5.)

For suggested answers, see Appendix A.

CONCEPT 30.3

The reproductive adaptations of angiosperms include flowers and fruits



Commonly known as flowering plants, angiosperms are seed plants with the reproductive structures called flowers and fruits. The name *angiosperm* (from the Greek *angion*, container) refers to seeds contained in fruits. Angiosperms are the most diverse and widespread of all plants, with more than 290,000 species (about 90% of all plant species).

Characteristics of Angiosperms

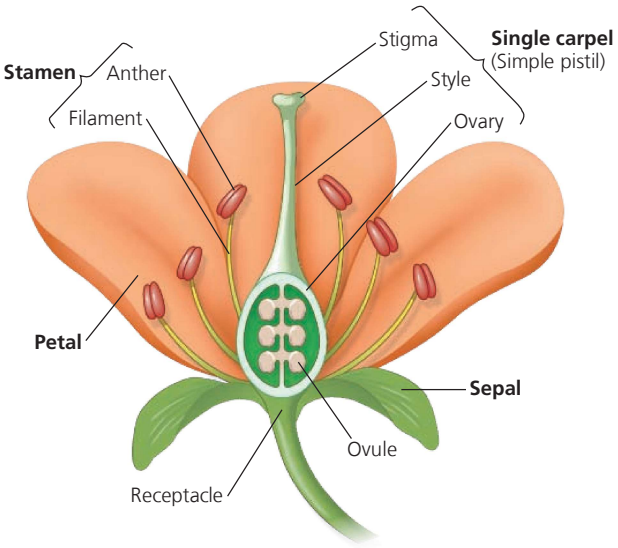
All angiosperms are classified in a single phylum, Anthophyta. Before considering the evolution of angiosperms, we will examine two of their key adaptations—flowers and fruits—and the roles of these structures in the angiosperm life cycle.

Flowers

The **flower** is a unique angiosperm structure that is specialized for sexual reproduction. In many angiosperm species, insects or other animals transfer pollen from one flower to the sex organs on another flower, which makes pollination more directed than the wind-dependent pollination of most species of gymnosperms. However, some angiosperms *are* wind-pollinated, particularly those species that occur in dense populations, such as grasses and tree species in temperate forests.

A flower is a specialized shoot that can have up to four types of modified leaves called floral organs: sepals, petals, stamens, and carpels **(Figure 30.8)**. Starting at the base of the flower are the **sepals**, which are usually green and enclose the flower before it opens (think of a rosebud). Interior to the sepals are the **petals**, which are brightly colored in most flowers and can aid in attracting pollinators. Flowers that are wind-pollinated, such as grasses, generally lack brightly colored parts. In all angiosperms, the sepals and petals are sterile floral organs, meaning that they do not produce sperm or eggs.

▼ Figure 30.8 The structure of an idealized flower.

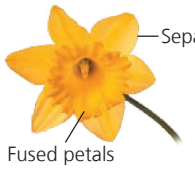


Within the petals are two types of fertile floral organs that produce spores, the stamens and carpels. Stamens and carpels are sporophylls, modified leaves that are specialized for reproduction. **Stamens** are microsporophylls: They produce microspores that develop into pollen grains containing male gametophytes. A stamen consists of a stalk called the **filament** and a terminal sac, the **anther**, where pollen is produced. **Carpels** are megasporophylls: They produce megaspores that give rise to female gametophytes. The carpel is the "container" mentioned earlier in which seeds are enclosed; as such, it is a key structure that distinguishes angiosperms from gymnosperms. At the tip of the carpel is a sticky **stigma** that receives pollen. A **style** leads from the stigma to a structure at the base of the carpel, the **ovary**; the ovary contains one or more ovules. As in gymnosperms, each angiosperm ovule contains a female gametophyte. If fertilized, an ovule develops into a seed.

A flower may have one or more carpels. In many species, multiple carpels are fused into one structure. The term **pistil** is sometimes used to refer to a single carpel (a simple pistil) or two or more fused carpels (a compound pistil). Flowers also vary in symmetry **(Figure 30.9)** and other aspects of shape, as

▼ Figure 30.9 Flower symmetry.

In radial symmetry, the sepals, petals, stamens, and carpels radiate out from a center. Any line through the central axis divides the flower into two equal parts.



Radial symmetry (daffodil)

In bilateral symmetry, the flower can only be divided into two equal parts by a single line.



Bilateral symmetry (orchid)

DRAW IT *Draw the single line that can divide the bilaterally symmetrical flower into two equal parts.*

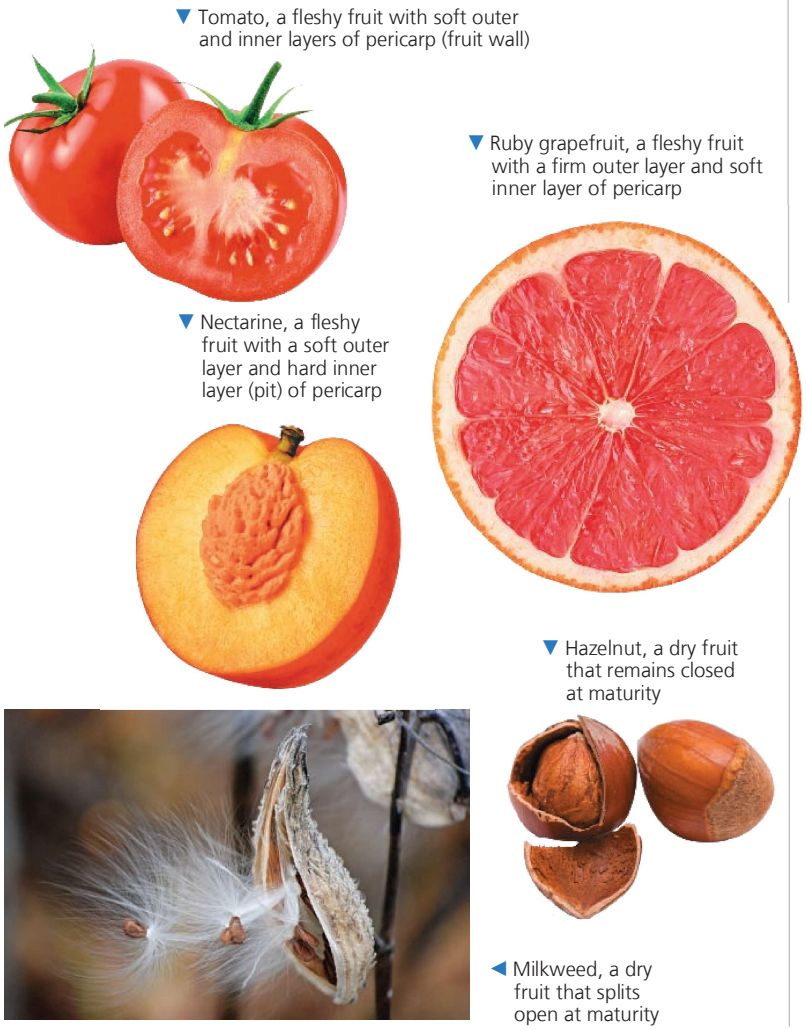
well as size, color, and odor. Much of this diversity results from adaptation to specific pollinators (see Figures 38.4 and 38.5).

Fruits

As seeds develop from ovules after fertilization, the ovary wall thickens and the ovary matures into a **fruit**. A pea pod is an example of a fruit, with seeds (mature ovules, the peas) encased in the ripened ovary (the pod).

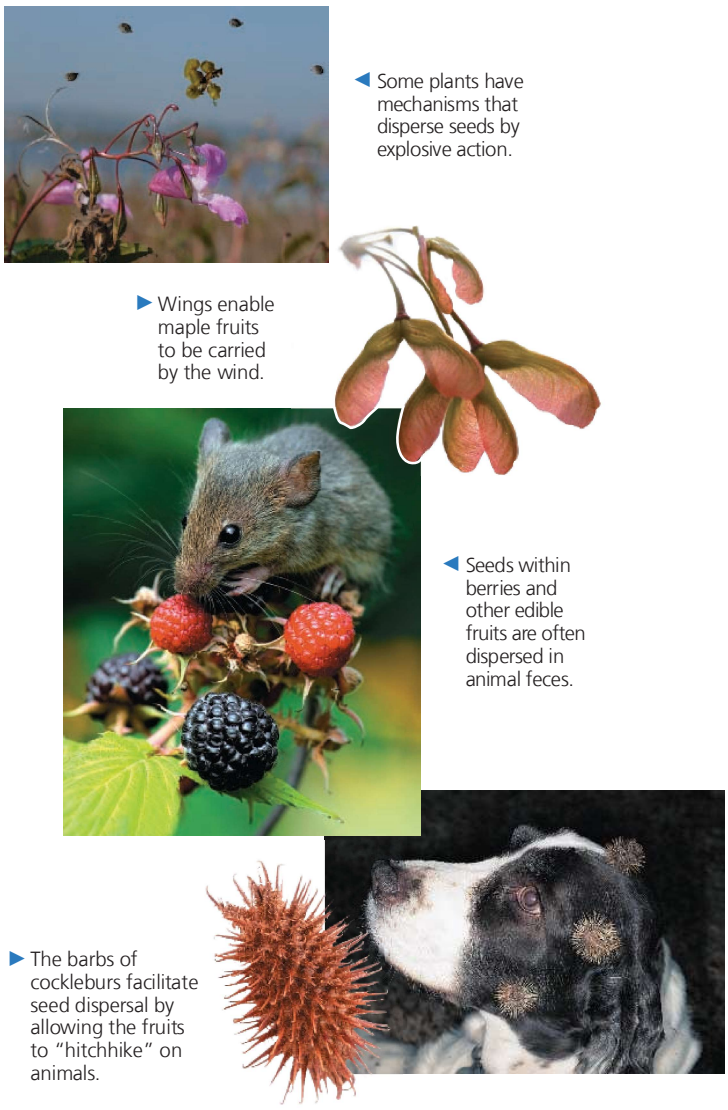
Fruits protect seeds and aid in their dispersal. Mature fruits can be either fleshy or dry **(Figure 30.10)**. Tomatoes, plums, and grapes are examples of fleshy fruits, in which the wall (pericarp) of the ovary becomes soft during ripening. Dry fruits include beans, nuts, and grains. Some dry fruits split open at maturity to release seeds, whereas others remain closed. The dry, wind-dispersed fruits of grasses, harvested while on the plant, are major staple foods for humans. The cereal grains of maize, rice, wheat, and other grasses, though easily mistaken for seeds, are each actually a fruit with a dry outer covering (the former wall of the ovary) that adheres to the seed coat of the seed within.

▼ Figure 30.10 Some variations in fruit structure.



As shown in **Figure 30.11**, various adaptations of fruits and seeds help to disperse seeds (see also Figure 38.12). The seeds of some flowering plants, such as dandelions and maples, are contained within fruits that function like parachutes or propellers, adaptations that enhance dispersal by wind. Some fruits, such as coconuts, are adapted to dispersal by water. And the seeds of many angiosperms are carried by animals. Some angiosperms have fruits modified as burrs that cling to animal fur (or the clothes of humans). Others produce edible fruits, which are usually nutritious, sweet tasting, and vividly colored, advertising their ripeness. When an animal eats the fruit, it digests the fruit's fleshy part, but the tough seeds usually pass unharmed through the animal's digestive tract. When the animal defecates, it may deposit the seeds, along with a supply of natural fertilizer, many kilometers from where the fruit was eaten.

▼ Figure 30.11 Fruit adaptations that enhance seed dispersal.



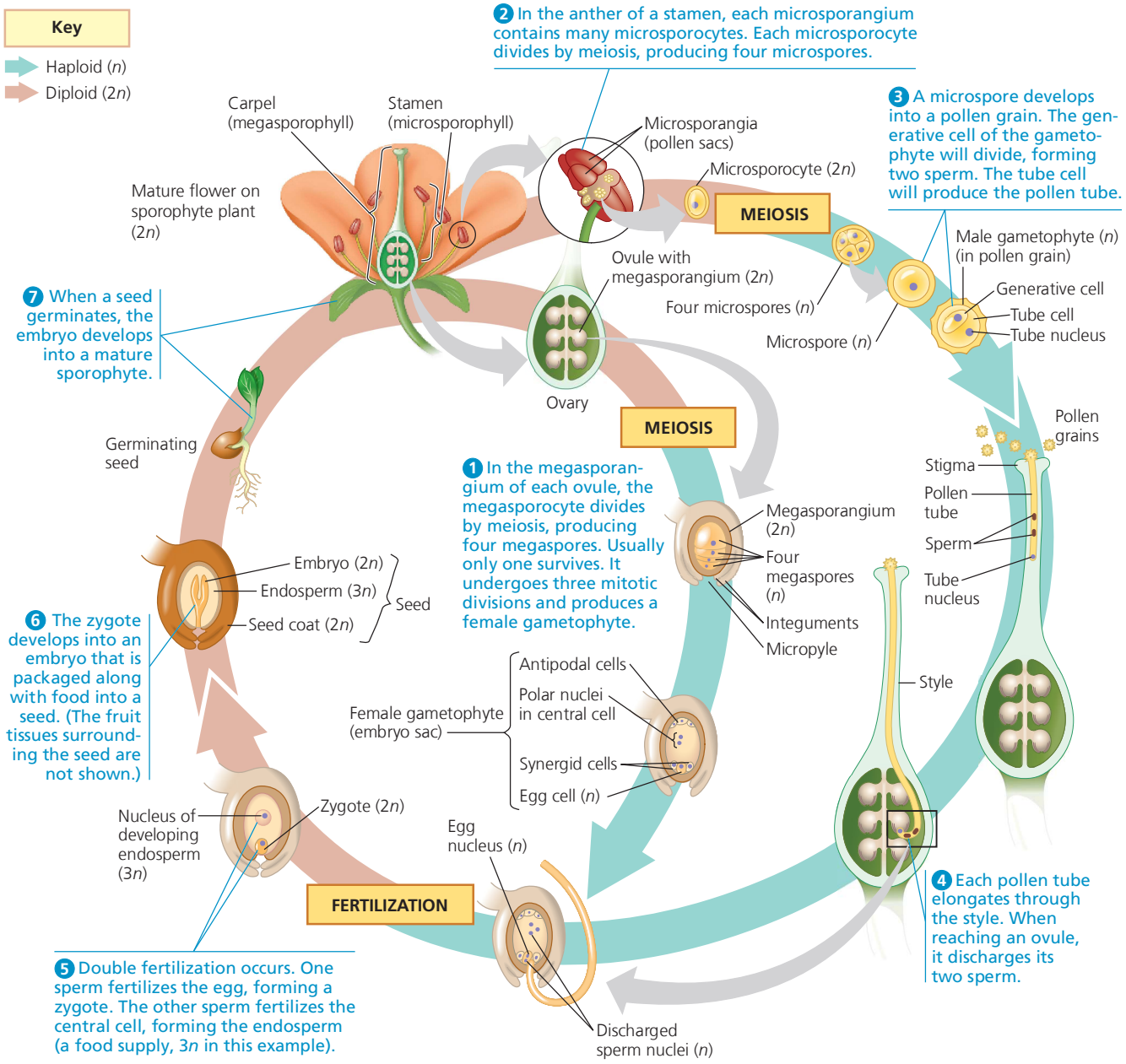
Mastering Biology ***Animation: Fruit Structure and Seed Dispersal***

The Angiosperm Life Cycle

You can follow a typical angiosperm life cycle in **Figure 30.12**. The flower of the sporophyte produces microspores that form male gametophytes and megaspores that form female gametophytes. The male gametophytes are in the pollen grains, which develop within microsporangia in the anthers. Each male gametophyte has two haploid cells: a *generative cell* that divides, forming two sperm, and a *tube cell* that produces a pollen tube. Each ovule, which develops in the ovary, contains a female gametophyte, also known as an **embryo sac**. The embryo sac consists of only a few cells, one of which is the egg.

After its release from the anther, the pollen is carried to the sticky stigma at the tip of a carpel. Although some flowers self-pollinate, most have mechanisms that ensure **cross-pollination**, which in angiosperms is the transfer of pollen from an anther of a flower on one plant to the stigma of a

▼ Figure 30.12 The life cycle of an angiosperm.



VISUAL SKILLS *Based on this figure, what is the maximum number of seeds this flower could produce? To produce that number of seeds, at least how many pollen grains would have to germinate?*

Mastering Biology Figure Walkthrough Animation: Angiosperm Life Cycle

flower on another plant of the same species. Cross-pollination enhances genetic variability. In some species, stamens and carpels of a single flower may mature at different times, or they may be so arranged that self-pollination is unlikely.

The pollen grain absorbs water and germinates after it adheres to the stigma of a carpel. The tube cell produces a pollen tube that grows down within the style of the carpel. After reaching the ovary, the pollen tube penetrates through the **micropyle**, a pore in the integuments of the ovule, and discharges two sperm cells into the female gametophyte (embryo sac). One sperm fertilizes the egg, forming a diploid zygote. The other sperm fuses with the two nuclei in the large central cell of the female gametophyte, producing a triploid cell (3*n*). This type of **double fertilization**, in which one fertilization event produces a zygote and the other produces a triploid cell, is unique to angiosperms.

After double fertilization, the ovule matures into a seed. The zygote develops into a sporophyte embryo with a rudimentary root and one or two seed leaves called **cotyledons**. The triploid central cell of the female gametophyte develops into **endosperm**, tissue rich in starch and other food reserves that nourish the developing embryo.

What is the function of double fertilization in angiosperms? One hypothesis is that double fertilization synchronizes the development of food storage in the seed with the development of the embryo. If a particular flower is not pollinated or sperm cells are not discharged into the embryo sac, fertilization does not occur, and neither endosperm nor embryo forms. So perhaps double fertilization is an adaptation that prevents flowering plants from squandering nutrients on infertile ovules.

Another type of double fertilization occurs in some gymnosperm species belonging to the phylum Gnetophyta. However, double fertilization in these species gives rise to two embryos rather than to an embryo and endosperm.

As you read earlier, the seed consists of the embryo, the endosperm, and a seed coat derived from the integuments. An ovary develops into a fruit as its ovules become seeds. After being dispersed, a seed may germinate if environmental conditions are favorable. The coat ruptures and the embryo emerges as a seedling, using food stored in the endosperm and cotyledons until it can produce its own food by photosynthesis.

Angiosperm Evolution

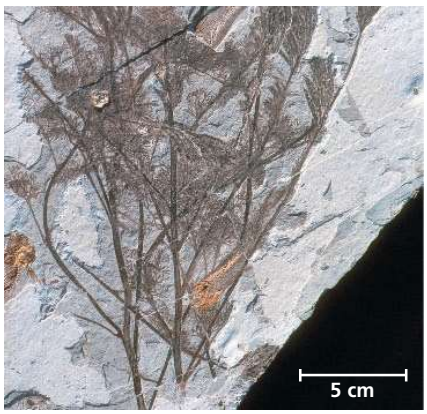
Charles Darwin once referred to the origin of angiosperms as an "abominable mystery." He was particularly troubled by the relatively sudden and geographically widespread appearance of angiosperms in the fossil record (about 100 million years ago, based on fossils known to Darwin). Recent fossil evidence and phylogenetic analyses have led to progress in solving Darwin's mystery, but we still do not fully understand how angiosperms arose from earlier seed plants.

Fossil Angiosperms

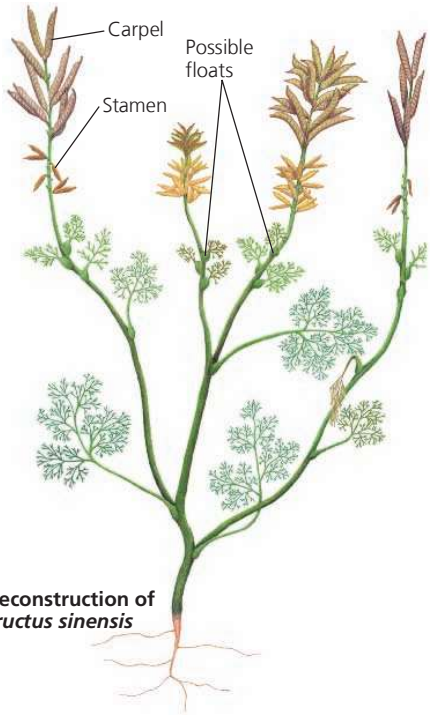
Angiosperms are now thought to have originated in the early Cretaceous period, about 140 million years ago. By the mid-Cretaceous (100 million years ago), angiosperms began to dominate some terrestrial ecosystems. Landscapes changed dramatically as conifers and other gymnosperms gave way to flowering plants in many parts of the world. The Cretaceous ended 66 million years ago with mass extinctions of dinosaurs and many other animal groups and with further increases in the diversity and importance of angiosperms.

What evidence suggests that angiosperms arose 140 million years ago? First, although pollen grains are common in rocks from the Jurassic period (201 to 145 million years ago), none of these pollen fossils have features characteristic of angiosperms, suggesting that angiosperms may have originated after the Jurassic. Indeed, the earliest fossils with distinctive angiosperm features are of 130-million-year-old pollen grains discovered in China, Israel, and England. Early fossils of larger flowering plant structures include those of *Archaefructus* **(Figure 30.13)** and *Leefructus*, both of which were discovered in China in rocks that are 125 million years old.

▼ Figure 30.13 An early flowering plant.



(a) *Archaefructus sinensis*, a 125-million-year-old fossil. This herbaceous species had simple flowers and bulbous structures that may have served as floats, suggesting it was aquatic. Recent phylogenetic analyses indicate that *Archaefructus* may belong to the water lily group.



(b) Artist's reconstruction of *Archaefructus sinensis*

Overall, early angiosperm fossils indicate that the group arose and began to diversify over a 20- to 30-million-year period—a less sudden event than was suggested by the fossils known during Darwin's lifetime.

Can we infer traits of the angiosperm common ancestor from traits found in early fossil angiosperms? *Archaefructus*, for example, was herbaceous and had bulbous structures that may have served as floats, suggesting it was aquatic. But investigating whether the angiosperm common ancestor was herbaceous and aquatic also requires examining fossils of other seed plants thought to have been closely related to angiosperms. All of those plants were woody, indicating that the common ancestor was probably woody and probably not aquatic. As we'll see, this conclusion has been supported by recent phylogenetic analyses.

Angiosperm Phylogeny

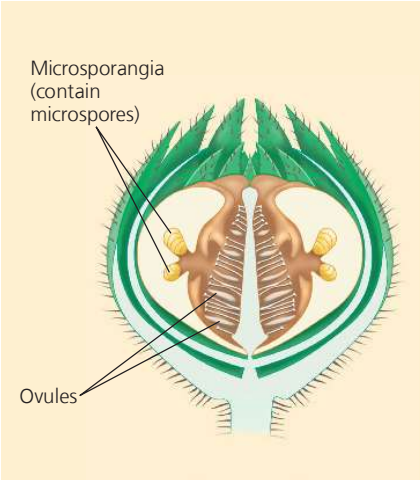
Molecular and morphological evidence suggests that extant gymnosperm lineages had diverged from the lineage leading to angiosperms by 305 million years ago. Note that this does not imply that angiosperms originated 305 million years ago, but that the most recent common ancestor of extant gymnosperms and angiosperms lived at that time. Indeed, angiosperms may be more closely related to several extinct lineages of woody seed plants than they are to gymnosperms. One such lineage is the Bennettitales, an extinct group with flowerlike structures that may have been pollinated by insects **(Figure 30.14a)**. However, the Bennettitales and other similar lineages of extinct woody seed plants did not have carpels or flowers and hence are not classified as angiosperms.

Making sense of the origin of angiosperms also depends on working out the order in which angiosperm clades diverged from one another. Here, dramatic progress has been made in recent years. Molecular and morphological evidence suggests that the shrub *Amborella trichopoda*, water lilies, and star anise are living representatives of lineages that diverged from other angiosperms early in the history of the group **(Figure 30.14b)**. *Amborella* is woody, supporting the conclusion mentioned earlier that the angiosperm common ancestor was probably woody. Like the Bennettitales, *Amborella*, water lilies, and star anise lack *vessel elements*, efficient water-conducting cells that are found in most present-day angiosperms. Overall, based on the features of ancestral species and angiosperms like *Amborella*, researchers have hypothesized that early angiosperms were woody shrubs that had small flowers and relatively simple water-conducting cells.

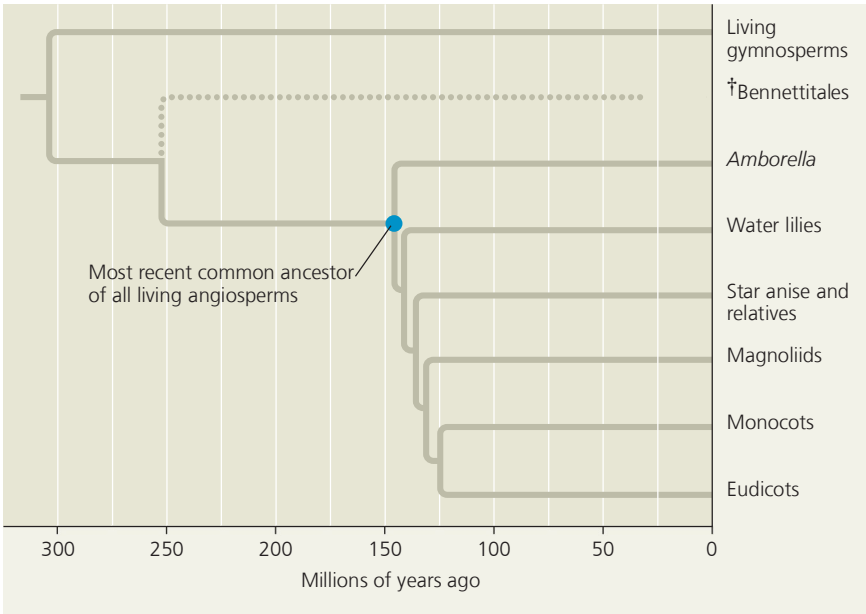
Evolutionary Links with Animals

Plants and animals have interacted for hundreds of millions of years, and those interactions have led to evolutionary change. For example, herbivores can reduce a plant's reproductive success by eating its roots, leaves, or seeds. As a result,

▼ Figure 30.14 Angiosperm evolutionary history.



(a) A close relative of the angiosperms? This reconstruction shows a longitudinal section through the flowerlike structures found in the Bennettitales, an extinct group of woody seed plants hypothesized to be more closely related to extant angiosperms than to extant gymnosperms.



(b) Angiosperm phylogeny. This tree represents a current hypothesis of angiosperm evolutionary relationships, based on morphological and molecular evidence. Angiosperms originated about 140 million years ago. The dotted line indicates the uncertain position of the Bennettitales, which may be the sister taxon to the angiosperms.

VISUAL SKILLS *Would the branching order of the phylogeny in (b) necessarily have to be redrawn if a 150-million-year-old fossil monocot were discovered? Explain.*

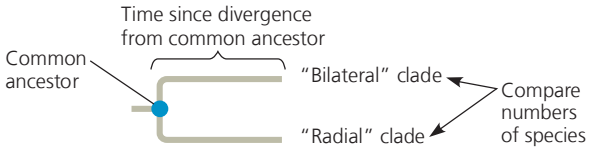


◀ Figure 30.15 A bee pollinating a bilaterally symmetrical flower. To harvest nectar from this Scottish broom flower, a honeybee must land as shown. This releases a tripping mechanism that arches the flower's stamens over the bee and dusts it with pollen. Later, some of this pollen may rub off onto the stigma of the next flower the bee visits.

Mastering Biology Video: Bee Pollinating

if an effective defense against herbivores originates in a group of plants, those plants may be favored by natural selection—as will herbivores that overcome this new defense. Plant-pollinator and other mutually beneficial interactions also can have such reciprocal evolutionary effects.

Plant-pollinator interactions also may have affected the rates at which new species form. Consider the impact of a flower's symmetry (see Figure 30.9). On a flower with bilateral symmetry, an insect pollinator can obtain nectar (a sugary solution secreted by flower glands) only when landing in a certain position **(Figure 30.15)**. This constraint makes it more likely that pollen is placed on a part of the insect's body that will come into contact with the stigma of a flower of the same species. Such specificity of pollen transfer reduces gene flow between diverging populations and could lead to increased rates of speciation in plants with bilateral symmetry. This hypothesis can be tested using the approach illustrated in this diagram:

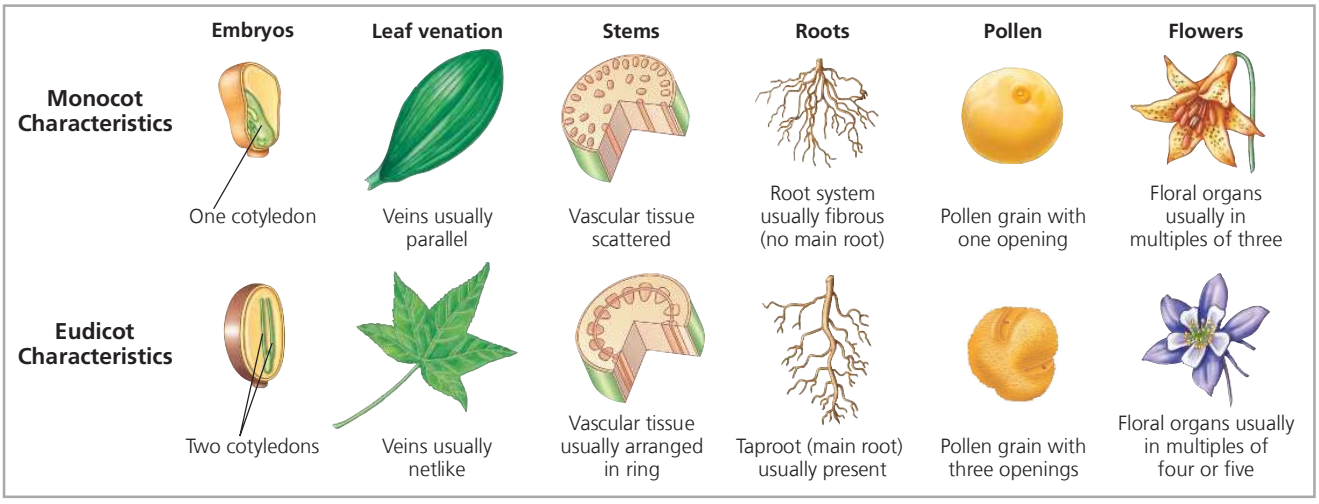


A key step in this approach is to identify cases in which a clade with bilaterally symmetric flowers shares an immediate common ancestor with a clade whose members have radially symmetric flowers. One recent study identified 19 pairs of closely related "bilateral" and "radial" clades. On average, the clade with bilaterally symmetric flowers had nearly 2,400 more species than did the related clade with radial symmetry. This result suggests that flower shape can affect the rate at which new species form, perhaps by affecting the behavior of insect pollinators. Overall, plant-pollinator interactions may have contributed to the increasing dominance of flowering plants in the Cretaceous period, making angiosperms centrally important to ecological communities.

Angiosperm Diversity

From their humble beginnings in the Cretaceous period, angiosperms have diversified into more than 290,000 living species. Until the late 1990s, most systematists divided flowering plants into two groups, based partly on the number of cotyledons, or seed leaves, in the embryo. Species with one cotyledon were called **monocots**, and those with two were called **dicots**. Other features, such as flower and leaf structure, were also used to define the two groups. Recent DNA studies, however, indicate that the species traditionally called dicots are paraphyletic. The vast majority of species once categorized as dicots form a large clade, now known as **eudicots** ("true" dicots). **Figure 30.16** compares the main characteristics of monocots and eudicots. The rest of the former dicots are now grouped into four small lineages. Three of these lineages—*Amborella*, water lilies, and star anise and relatives—are informally called **basal angiosperms** because they diverged from other angiosperms early in the history of the group (see Figure 30.14b). A fourth lineage, the **magnoliids**, evolved later. **Figure 30.17** provides an overview of angiosperm diversity.

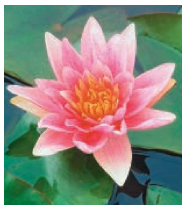
▼ Figure 30.16 Characteristics of monocots and eudicots.



▼ Figure 30.17 Exploring Angiosperm Diversity

Basal Angiosperms

Surviving basal angiosperms consist of three lineages comprising only about 100 species. The first lineage to have diverged from other angiosperms is represented today by a single species, *Amborella trichopoda* (right). The other surviving lineages diverged later: a clade that includes water lilies and a clade consisting of the star anise and its relatives.



◀ **Water lily (*Nymphaea "Rene Gerard"*).** Species of water lilies are found in aquatic habitats throughout the world. Water lilies belong to a clade that diverged from other angiosperms early in the group's history.



◀ **Star anise (*Illicium*).** This genus belongs to a third surviving lineage of basal angiosperms.

Amborella trichopoda. ▶ This small shrub, found only on the South Pacific island of New Caledonia, may be the sole survivor of a branch at the base of the angiosperm tree.



Magnoliids

Magnoliids consist of about 8,500 species, most notably magnolias, laurels, and black pepper plants. They include both woody and herbaceous species. Although they share some traits with basal angiosperms, such as a typically spiral rather than whorled arrangement of floral organs, magnoliids are more closely related to eudicots and monocots.



◀ **Southern magnolia (*Magnolia grandiflora*).** This member of the magnolia family is a large tree. The variety of southern magnolia shown here, called "Goliath," has flowers that measure up to about a foot across.

Monocots

About one-quarter of angiosperm species are monocots —about 72,000 species. Some of the largest groups are the orchids, grasses, and palms. Grasses include some of the most agriculturally important crops, such as maize, rice, and wheat.



◀ **Orchid (*Paphiopedilum callosum*)**

Barley (*Hordeum vulgare*), a grass ▶

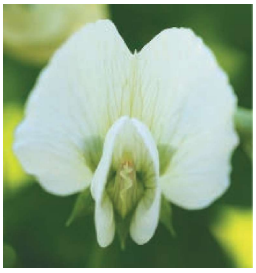




▲ **Pygmy date palm (*Phoenix roebelenii*)**

Eudicots

More than two-thirds of angiosperm species are eudicots—roughly 210,000 species. The largest group is the legume family, which includes such crops as peas and beans. Also important economically is the rose family, which includes many plants with ornamental flowers as well as some species with edible fruits, such as strawberry plants and apple and pear trees. Most of the familiar flowering trees are eudicots, such as oak, walnut, maple, willow, and birch.



◀ **Snow pea (*Pisum sativum*), a legume**

Dog rose (*Rosa canina*), a wild rose ▶





▲ **Armenian oak (*Quercus pontica*)**

CONCEPT CHECK 30.3

1. It is said that an oak is an acorn's way of making more acorns. Write an explanation that includes these terms: sporophyte, gametophyte, ovule, seed, ovary, and fruit.
2. Compare and contrast a pine cone and a flower in terms of structure and function.
3. **WHAT IF?** Do speciation rates in closely related clades of flowering plants show that flower shape is *correlated with* the rate at which new species form or that flower shape is *responsible for* this rate? Explain.

For suggested answers, see Appendix A.

CONCEPT 30.4

Human welfare depends on seed plants

In forests and on farms, seed plants are key sources of food, fuel, wood products, and medicine. Our reliance on them makes the preservation of plant diversity critical.

Products from Seed Plants

Most of our food comes from angiosperms. Just six crops—maize, rice, wheat, potatoes, cassava, and sweet potatoes—yield 80% of all the calories consumed by humans. We also depend on angiosperms to feed livestock: It takes 5–7 kg of grain to produce 1 kg of grain-fed beef.

Today's crops are the products of artificial selection—the result of plant domestication that began about 12,000 years ago. To appreciate the scale of this transformation, note how the number and size of seeds in domesticated plants are greater than those of their wild relatives, as in the case of maize and the grass teosinte (see Figure 38.16). Scientists can glean information about domestication by comparing the genes of crops with those of wild relatives. With maize, dramatic changes such as increased cob size and loss of the hard coating around teosinte kernels may have been initiated by as few as five mutations.

Flowering plants also provide other edible products. Two popular beverages come from tea leaves and coffee beans, and you can thank the cacao tree for cocoa and chocolate. Spices are derived from various plant parts, such as flowers (cloves, saffron), fruits and seeds (vanilla, black pepper, mustard), leaves (basil, mint, sage), and even bark (cinnamon).

Many seed plants are sources of wood, which is absent in all living seedless plants. Wood consists of tough-walled xylem cells (see Figure 35.22). It is the primary source of fuel for much of the world, and wood pulp, typically derived from conifers such as fir and pine, is used to make paper. Wood remains the most widely used construction material.

For centuries, humans have also depended on seed plants for medicines. Many cultures use herbal remedies, and scientists have extracted and identified medicinally active compounds from many of these plants and later synthesized them. Willow leaves and bark have long been used in pain-relieving remedies, including prescriptions by the Greek physician Hippocrates. In the 1800s, scientists traced the willow's medicinal property to the chemical salicin. A synthesized derivative, acetylsalicylic acid, is what we call aspirin. Plants are also a direct source of medicinal compounds **(Table 30.1)**. In the United States, about 25% of prescription drugs contain an active ingredient from plants, usually seed plants.

Table 30.1 Examples of Plant-Derived Medicines

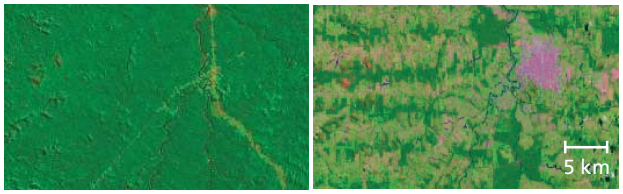
Compound	Source	Use
Atropine	Belladonna plant	Eye pupil dilator
Digitalin	Foxglove	Heart medication
Menthol	Eucalyptus tree	Throat soother
Quinine	Cinchona tree	Malaria preventive
Taxol	Pacific yew	Ovarian cancer drug
Tubocurarine	Curare tree	Muscle relaxant
Vinblastine	Periwinkle	Leukemia drug

Threats to Plant Diversity

Although plants may be a renewable resource, plant diversity is not. The exploding human population and its demand for space and resources are threatening plant species across the globe. The problem is especially severe in the tropics, where more than two-thirds of the human population live and where population growth is fastest. About 63,000 km^2 (15 million acres) of tropical rain forest are cleared each year **(Figure 30.18)**, a rate that would completely eliminate the remaining 11 million km^2 of tropical forests in 175 years. The loss of forests reduces the absorption of atmospheric carbon dioxide (CO_2) that occurs during photosynthesis, potentially contributing to global warming. Also, as forests disappear, so do large numbers of plant species. Of course, once a species becomes extinct, it can never return.

The loss of plant species is often accompanied by the loss of insects and other rain forest animals. Scientists estimate that if current rates of loss in the tropics and elsewhere

▼ Figure 30.18 Clear-cutting of tropical forests. Over the past several hundred years, nearly half of Earth's tropical forests have been cut down and converted to farmland and other uses. A satellite image from 1975 (left) shows a dense forest in Brazil. By 2012, much of this forest had been cut down. Deforested and urban areas are shown as light purple.



continue, 50% or more of Earth's species will become extinct within the next few centuries. Such losses would constitute a global mass extinction, rivaling the Permian and Cretaceous mass extinctions and forever changing the evolutionary history of plants (and many other organisms).

Many people have ethical concerns about contributing to the extinction of species. In addition, there are practical reasons to be concerned about the loss of plant diversity. So far, we have explored the potential uses of only a tiny fraction of the more than 325,000 known plant species. For example, almost all our food is based on the cultivation of only about two dozen species of seed plants. And fewer than 5,000 plant species have been studied as potential sources of medicines. The tropical rain forest may be a medicine chest of healing plants that could be extinct before we even know they exist. If we begin to view rain forests and other ecosystems as living treasures that can regenerate only slowly, we may learn to harvest their products at sustainable rates.

CONCEPT CHECK 30.4

1. Explain why plant diversity can be considered a nonrenewable resource.
2. **WHAT IF?** How could phylogenies be used to help researchers search more efficiently for novel medicines derived from seed plants?

For suggested answers, see Appendix A.

30 Chapter Review



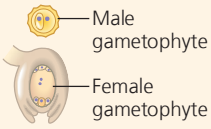
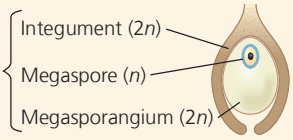
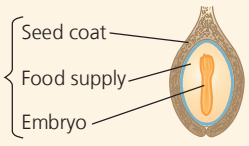
Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

CONCEPT 30.1

Seeds and pollen grains are key adaptations for life on land *(pp. 637–639)*

Five Derived Traits of Seed Plants	
Reduced gametophytes	Microscopic male and female gametophytes (*n*) are nourished and protected by the sporophyte (2*n*) 
Heterospory	Microspore (gives rise to a male gametophyte)  Megaspore (gives rise to a female gametophyte) 
Ovules	Ovule (gymnosperm) 
Pollen	Pollen grains make water unnecessary for fertilization 
Seeds	Seeds: survive better than unprotected spores, can be transported long distances 

Describe how the parts of an ovule (integument, megaspore, megasporangium) correspond to the parts of a seed.

CONCEPT 30.2

Gymnosperms bear "naked" seeds, typically on cones *(pp. 640–644)*

- Dominance of the sporophyte generation, the development of seeds from fertilized ovules, and the role of pollen in transferring sperm to ovules are key features of a typical gymnosperm life cycle.
- Gymnosperms appear early in the plant fossil record and dominated many Mesozoic terrestrial ecosystems. Living seed plants can be divided into two monophyletic groups: gymnosperms and angiosperms. Extant gymnosperms include cycads, *Ginkgo biloba*, gnetophytes, and **conifers**.

Although there are just over 1,000 species of gymnosperms, the group is still very successful in terms of its evolutionary longevity, adaptations, and geographic distribution. Explain.

CONCEPT 30.3

The reproductive adaptations of angiosperms include flowers and fruits *(pp. 644–651)*

- **Flowers** generally consist of four types of modified leaves: **sepals, petals, stamens** (which produce pollen), and **carpels** (which produce ovules). **Ovaries** ripen into **fruits**, which often carry seeds by wind, water, or animals to new locations.
- Flowering plants originated about 140 million years ago, and by the mid-Cretaceous (100 mya) had begun to dominate some terrestrial ecosystems. Fossils and phylogenetic analyses offer insights into the origin of flowers.
- Several groups of **basal angiosperms** have been identified. Other major clades of angiosperms include **magnoliids, monocots**, and **eudicots**.
- Pollination and other interactions between angiosperms and animals may have contributed to the success of flowering plants during the last 100 million years.

Explain why Darwin called the origin of angiosperms an "abominable mystery," and describe what has been learned from fossil evidence and phylogenetic analyses.

CONCEPT **30.4**

Human welfare depends on seed plants *(pp. 651–652)*

- Humans depend on seed plants for products such as food, wood, and many medicines.
- Destruction of habitat threatens the extinction of many plant species and the animal species they support.

? *Explain why destroying the remaining tropical forests might harm humans and lead to a mass extinction.*

TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

1. Where in an angiosperm would you find a megasporangium?
(A) in the style of a flower
(B) enclosed in the stigma of a flower
(C) within an ovule contained within an ovary of a flower
(D) packed into pollen sacs within the anthers found on a stamen

2. Which of the following is a key feature of seed plants facilitating life on land?
(A) homospory
(B) pollen
(C) reduced sporophytes
(D) spores

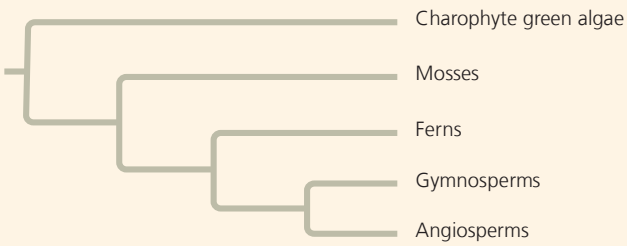
3. In angiosperms, which of the following is correctly paired with its chromosome count?
(A) microspore—n
(B) zygote—n
(C) egg—$2n$
(D) megaspore—$2n$

4. Which of the following is a characteristic that distinguishes gymnosperms and angiosperms from other plants?
(A) alternation of generations
(B) independent gametophytes
(C) vascular tissue
(D) ovules

5. Which of the following are present in angiosperms but not in gymnosperms?
(A) seeds
(B) pollen
(C) ovaries
(D) ovules

Levels 3-4: Applying/Analyzing

6. **DRAW IT** Use the letters a–d to label where on the phylogenetic tree each of the following derived characters appears.
a. flowers
b. embryos
c. seeds
d. vascular tissue



7. **EVOLUTION CONNECTION** The history of life has been punctuated by several mass extinctions. For example, the impact of a meteorite may have wiped out most of the dinosaurs and many forms of marine life at the end of the Cretaceous period (see Concept 25.4). Fossils indicate that plants were less severely affected by this mass extinction. What adaptations may have enabled plants to withstand this disaster better than animals?

Levels 5-6: Evaluating/Creating

8. **SCIENTIFIC INQUIRY • DRAW IT** As will be described in detail in Concept 38.1, the female gametophyte of angiosperms typically has seven cells, one of which, the central cell, contains two haploid nuclei. After double fertilization, the central cell develops into endosperm, which is triploid. Because magnoliids, monocots, and eudicots typically have female gametophytes with seven cells and triploid endosperm, scientists assumed that this was the ancestral state for angiosperms. Consider, however, the following recent discoveries:
- Our understanding of angiosperm phylogeny has changed to that shown in Figure 30.14b.
- *Amborella trichopoda* has eight-celled female gametophytes and triploid endosperm.
- Water lilies and star anise have four-celled female gametophytes and diploid endosperm.

(a) Draw a phylogeny of the angiosperms (see Figure 30.14b), incorporating the data given above about the number of cells in female gametophytes and the ploidy of the endosperm. Assume that all of the star anise relatives have four-celled female gametophytes and diploid endosperm.
(b) What does your labeled phylogeny suggest about the evolution of the female gametophyte and endosperm in angiosperms?

9. **WRITE ABOUT A THEME: ORGANIZATION** Cells are the basic units of structure and function in all organisms. A key feature in the life cycle of plants is the alternation of multicellular haploid and diploid generations. Imagine a lineage of flowering plants in which mitotic cell division did not occur between the events of meiosis and fertilization (see Figure 30.12). In a short essay (100–150 words), describe how this change in the timing of cell division would affect the structure and life cycle of plants in this lineage.

10. **SYNTHESIZE YOUR KNOWLEDGE**



This photograph shows a milkweed seed in flight. Describe how seeds and other adaptations in seed plants contributed to the rise of seed plants and their dominant role in plant communities today.

For selected answers, see Appendix A.

Explore Scientific Papers with Science in the Classroom AAAS
How have Earth's forests changed over time?
Go to "Seeing the Forest for the Trees"
at www.scienceintheclassroom.org.
Instructors: Questions can be assigned in Mastering Biology.

31 Fungi

KEY CONCEPTS

31.1 **Fungi are heterotrophs that feed by absorption** *p. 655*

31.2 **Fungi produce spores through sexual or asexual life cycles** *p. 657*

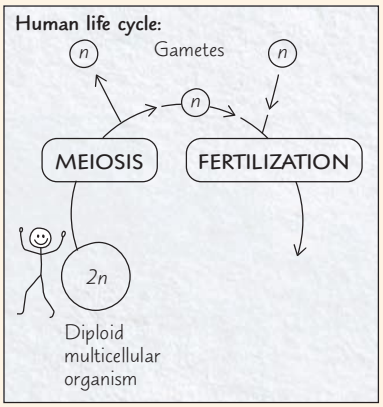
31.3 **The ancestor of fungi was an aquatic, single-celled, flagellated protist** *p. 659*

31.4 **Fungi have radiated into a diverse set of lineages** *p. 660*

31.5 **Fungi play key roles in nutrient cycling, ecological interactions, and human welfare** *p. 667*

Study Tip

Draw a diagram: To help you recognize key differences between the life cycles of fungi and humans, draw and label simple diagrams like the partial example shown here depicting the life stages at which meiosis, mitosis, gamete formation, a multicellular organism, and fertilization occur in humans and in fungi.



Go to Mastering Biology

For Students (in eText and Study Area)
- Get Ready for Chapter 31
- Animation: Life Cycle of a Mushroom

For Instructors to Assign (in Item Library)
- Activity: Fungal Reproduction and Nutrition
- Scientific Skills Exercise: Synthesizing Information from Multiple Data Sets



Figure 31.1 These little mushrooms are just the small aboveground extension of a vast network of filaments located below the forest floor. Such underground fungal networks, called mycelia, in some cases link mushrooms that are hundreds of meters apart. In fact, the largest known mycelium spreads beneath 965 hectares of forest—more than the area of 1,800 football fields.

How do structure and function in fungi relate to their role in ecosystems?

As they grow, multicellular fungi extend filaments called **hyphae** into their surroundings.

Spores enable fungi to colonize new envrironments. The spores germinate and grow when conditions are favorable.

Spores

Hyphae

Hyphae **secrete enzymes** that break down organic matter, releasing nutrients.

Nutrients

Hyphae **absorb** the released nutrients.

Almost any organic molecule can be digested by at least some fungi, making them highly effective **decomposers in ecosystems.**

The hidden network of fungal filaments in Figure 31.1 is a fitting symbol of the neglected grandeur of the kingdom Fungi. Most of us are barely aware of these eukaryotes beyond the mushrooms we eat or the occasional brush with athlete's foot. Yet fungi are a huge and important component of the biosphere. Some fungi are exclusively single-celled, though most have complex multicellular bodies. These diverse organisms are found in just about every imaginable terrestrial and aquatic habitat.

Fungi are not only diverse and widespread but also essential for the well-being of most ecosystems. They break down organic material and recycle nutrients, allowing other organisms to assimilate essential chemical elements. In this chapter, we will investigate the structure and evolutionary history of fungi, survey the major groups of fungi, and discuss their ecological and commercial significance.

CONCEPT 31.1

Fungi are heterotrophs that feed by absorption

Despite their vast diversity, all fungi share some key traits—most importantly, the way they derive nutrition. Another key characteristic of many fungi is that they grow by forming multicellular filaments, a body structure that plays an important role in how they obtain food.

Nutrition and Ecology

Like animals, fungi are heterotrophs: They cannot make their own food as plants and algae can. But unlike animals, fungi do not ingest (eat) their food. Instead, a fungus absorbs nutrients from the environment outside of its body. Many fungi do this by secreting hydrolytic enzymes into their surroundings. These enzymes break down complex molecules to smaller organic compounds that the fungi can absorb into their cells and use. Other fungi use enzymes to penetrate the walls of cells, enabling the fungi to absorb nutrients from the cells. Collectively, the different enzymes found in various fungal species can digest compounds from a wide range of sources, living or dead.

This diversity of food sources corresponds to the varied roles of fungi in ecological communities: Different species live as decomposers, parasites, or mutualists. Fungi that are decomposers break down and absorb nutrients from nonliving organic material, such as fallen logs, animal corpses, and the wastes of organisms. Parasitic fungi absorb nutrients from the cells of living hosts. Some parasitic fungi are pathogenic, including many species that cause diseases in plants and others that cause diseases in animals. Mutualistic fungi also absorb nutrients from a host, but they reciprocate with actions that benefit the host. For example, mutualistic fungi that live within the digestive tracts of certain termite species use their enzymes to break down wood, as do mutualistic protists in other termites (see Figure 28.29).

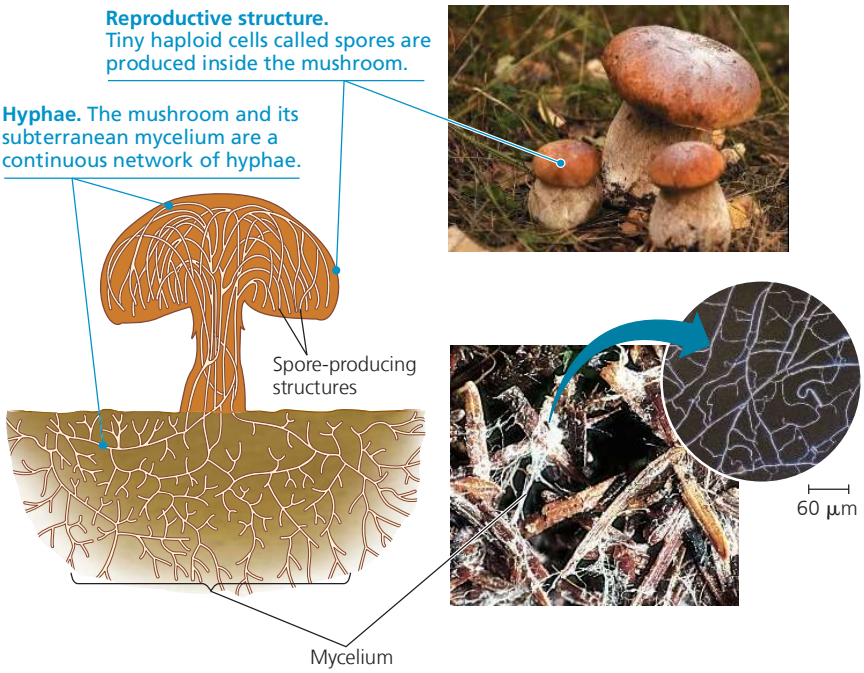
The versatile enzymes that enable fungi to digest a wide range of food sources are not the only reason for their ecological success. Another important factor is how their body structure increases the efficiency of nutrient absorption.

Body Structure

The most common fungal body structures are multicellular filaments and single cells (**yeasts**). Many fungal species can grow as both filaments and yeasts, but even more grow only as filaments; relatively few species grow only as single-celled yeasts. Yeasts often inhabit moist environments, including plant sap and animal tissues, where there is a ready supply of soluble nutrients, such as sugars and amino acids.

The morphology of multicellular fungi enhances their ability to grow into and absorb nutrients from their surroundings **(Figure 31.2)**. The bodies of these fungi typically form a

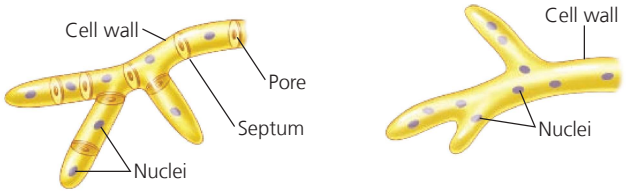
▼ **Figure 31.2 Structure of a multicellular fungus.** The top photograph shows the sexual structures, in this case called mushrooms, of the penny bun fungus (*Boletus edulis*). The bottom photograph shows a mycelium growing on fallen conifer needles. The inset SEM shows hyphae.



? *Although the mushrooms in the top photograph appear to be different individuals, could their DNA be identical? Explain.*

Mastering Biology **Animation: Fungal Growth and Nutrition**

▼ **Figure 31.3 Two forms of hyphae.**



(a) Septate hypha **(b) Coenocytic hypha**

network of tiny filaments called **hyphae** (singular, *hypha*). Hyphae consist of tubular cell walls surrounding the plasma membrane and cytoplasm of the cells. The cell walls are strengthened by **chitin**, a strong but flexible polysaccharide. Chitin-rich walls can enhance feeding by absorption. As a fungus absorbs nutrients from its environment, the concentrations of those nutrients in its cells increases, causing water to move into the cells by osmosis. The movement of water into fungal cells creates pressure that could cause their cells to burst if they were not surrounded by a chitin-strengthened, rigid cell wall.

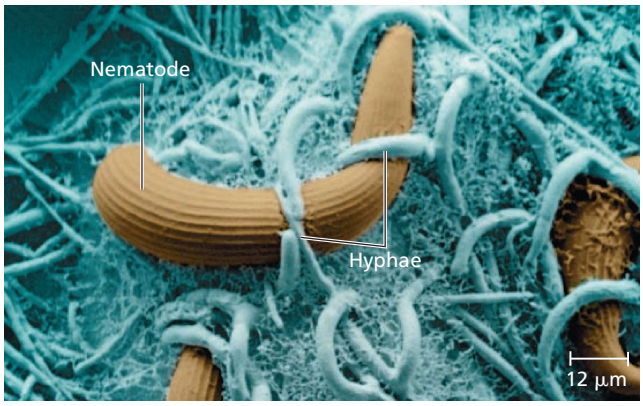
Another important structural feature of most fungi is that their hyphae are divided into cells by cross-walls, or **septa** (singular, *septum*) **(Figure 31.3a)**. Septa generally have pores large enough to allow ribosomes, mitochondria, and even nuclei to flow from cell to cell. Some fungi lack septa **(Figure 31.3b)**. Known as **coenocytic fungi**, these organisms consist of a continuous cytoplasmic mass having hundreds or thousands of nuclei. The coenocytic condition results from the repeated division of nuclei without cytokinesis.

Fungal hyphae form an interwoven mass called a **mycelium** (plural, *mycelia*) that infiltrates the material on which the fungus feeds (see Figure 31.2). The structure of a mycelium maximizes its surface-to-volume ratio, making feeding very efficient. Just 1 cm^3 of rich soil may contain as much as 1 km of hyphae with a total surface area of 300 cm^2 in contact with the soil. A fungal mycelium grows rapidly, as proteins and other materials synthesized by the fungus move through cytoplasmic streaming to the tips of the extending hyphae. The fungus concentrates its energy and resources on adding hyphal length and thus overall absorptive surface area, rather than on increasing hyphal girth. Multicellular fungi are not motile in the typical sense—they cannot run, swim, or fly in search of food or mates. However, as they grow, such fungi can move into new territory, swiftly extending the tips of their hyphae.

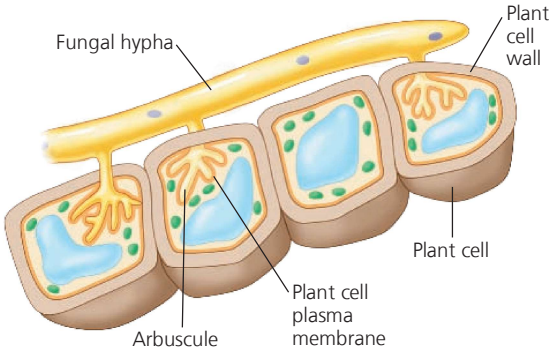
Specialized Hyphae in Mycorrhizal Fungi

Some fungi have specialized hyphae that allow them to feed on living animals **(Figure 31.4a)**, while others have modified hyphae called *haustoria* that enable them to extract nutrients from plants. Our focus here, however, will be on fungi that have specialized branching hyphae such as **arbuscules (Figure 31.4b)** through which fungi exchange nutrients with their plant hosts. Such mutually beneficial relationships between fungi and plant roots are called **mycorrhizae** (the term means "fungus roots").

▼ **Figure 31.4 Specialized hyphae.**



(a) Hyphae adapted for trapping and killing prey. In *Arthrobotrys*, a soil fungus, portions of the hyphae are modified as hoops that can constrict around a nematode (roundworm) in less than a second. The growing hyphae then penetrate the worm's body, and the fungus digests its prey's inner tissues (SEM).



(b) Arbuscules. Some mutualistic fungi have specialized hyphae called arbuscules that can exchange nutrients with living plant cells. Arbuscules remain separated from a plant cell's cytoplasm by the plasma membrane of the plant cell (orange).

Mycorrhizal fungi (fungi that form mycorrhizae) can improve delivery of phosphate ions and other minerals to plants because the vast mycelial networks of the fungi are more efficient than the plants' roots at acquiring these minerals from the soil. In exchange, the plants supply the fungi with organic nutrients such as carbohydrates.

There are two main types of mycorrhizal fungi (see Figure 37.14). **Ectomycorrhizal fungi** (from the Greek *ektos*, out) form sheaths of hyphae over the surface of a root and typically grow into the extracellular spaces of the root cortex. **Arbuscular mycorrhizal fungi** extend arbuscules through the root cell wall and into tubes formed by invagination (pushing inward, as in Figure 31.4b) of the root cell plasma membrane. In the **Scientific Skills Exercise**, you'll compare genomic data from fungi that form mycorrhizae and fungi that do not.

Mycorrhizae are enormously important both in natural ecosystems and in agriculture. Almost all vascular plants have mycorrhizae and rely on their fungal partners for essential nutrients. Foresters commonly inoculate pine seedlings

Scientific Skills Exercise

Interpreting Genomic Data and Generating Hypotheses



What Can Genomic Analysis of a Mycorrhizal Fungus Reveal About Mycorrhizal Interactions? The first genome of a mycorrhizal fungus to be sequenced was that of the basidiomycete *Laccaria bicolor* (see photo). In nature, *L. bicolor* is a common ectomycorrhizal fungus of trees such as poplar and fir, as well as a free-living soil organism. In forest nurseries, it is often added to soil to enhance seedling growth. The fungus can easily be grown alone in culture and can establish mycorrhizae with tree roots in the laboratory. Researchers hope that studying the genome of *Laccaria* will yield clues to the processes by which it interacts with its mycorrhizal partners—and by extension, to mycorrhizal interactions involving other fungi.

How the Study Was Done Using the whole-genome shotgun method (see Figure 21.2) and bioinformatics, researchers sequenced the genome of *L. bicolor* and compared it with the genomes of some nonmycorrhizal basidiomycete fungi. The team used microarrays to compare gene expression levels for different protein-coding genes and for the same genes in a mycorrhizal mycelium and a free-living mycelium. They could thus identify the genes for fungal proteins that are made specifically in mycorrhizae.

Data from the Study

Table 1 Numbers of Genes in *L. bicolor* and Four Nonmycorrhizal Fungal Species

	L. bicolor	1	2	3	4
Protein-coding genes	20,614	13,544	10,048	7,302	6,522
Genes for membrane transporters	505	412	471	457	386
Genes for small secreted proteins (SSPs)	2,191	838	163	313	58

Table 2 *L. bicolor* Genes Most Highly Upregulated in Ectomycorrhizal Mycelium (ECM) of Douglas Fir or Poplar Versus Free-Living Mycelium (FLM)

Protein ID	Protein Feature or Function	Douglas Fir ECM/FLM Ratio	Poplar ECM/FLM Ratio
298599	SSP	22,877	12,913
293826	Enzyme inhibitor	14,750	17,069
333839	SSP	7,844	1,931
316764	Enzyme	2,760	1,478

Data from F. Martin et al., The genome of *Laccaria bicolor* provides insights into mycorrhizal symbiosis, *Nature* 452:88–93 (2008).

INTERPRET THE DATA

1. **(a)** In Table 1, which fungal species has the most genes encoding membrane transporters (membrane transport proteins; see Concept 7.2)? **(b)** Why might these genes be of particular importance to *L. bicolor*?
2. The phrase "small secreted proteins" (SSPs) refers to proteins less than 100 amino acids in length that the fungi secrete; their function is not yet known. **(a)** Describe the Table 1 data on SSPs. **(b)** The researchers found that the SSP genes shared a common feature that indicated the encoded proteins were destined for secretion. Based on Figure 17.22 and the text discussion of that figure, predict what this common feature of the SSP genes was. **(c)** Suggest a hypothesis for the roles of SSPs in mycorrhizae.
3. Table 2 shows data from gene expression studies for the four *L. bicolor* genes whose transcription was most increased ("upregulated") in mycorrhizae. **(a)** For the gene encoding the first protein listed, what does the number 22,877 indicate? **(b)** Do the data in Table 2 support your hypothesis in question 2(c)? Explain. **(c)** Compare the data for poplar mycorrhizae with those for Douglas fir and hypothesize what might account for any differences.

Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

with mycorrhizal fungi to promote growth. In the absence of human intervention, mycorrhizal fungi colonize soils by dispersing haploid cells called **spores** that form new mycelia after germinating. Spore dispersal is a key component of how fungi reproduce and spread to new areas, as we discuss next.

CONCEPT CHECK 31.1

1. Compare and contrast the nutritional mode of a fungus with your own nutritional mode.
2. **WHAT IF?** Suppose a certain fungus is a mutualist that lives within an insect host, yet its ancestors were parasites that grew in and on the insect's body. What derived traits might you find in this mutualistic fungus?
3. **MAKE CONNECTIONS** Review Figure 10.3 and Figure 10.5. If a plant has mycorrhizae, where might carbon that enters the plant's stomata as CO_2 eventually be deposited: in the plant, in the fungus, or both? Explain.

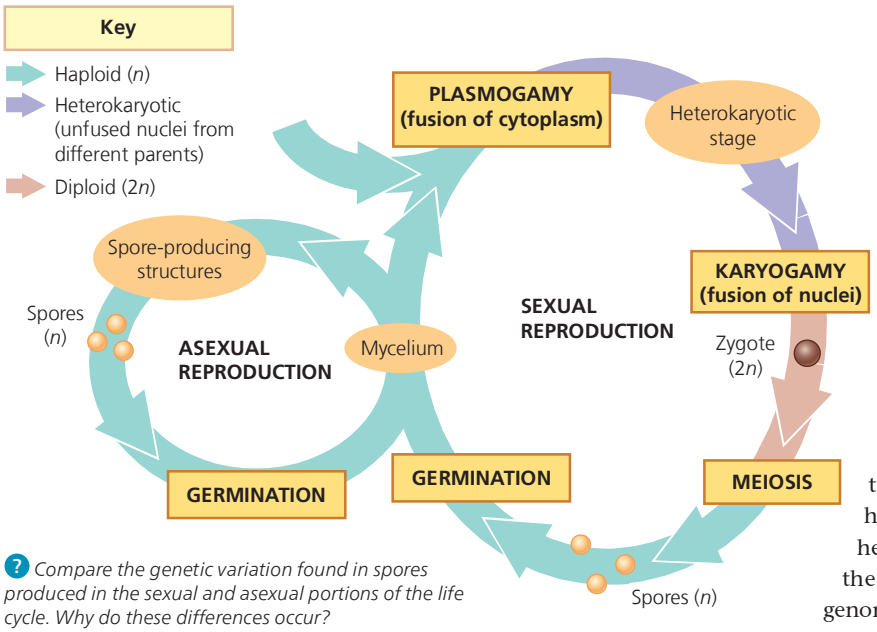
For suggested answers, see Appendix A.

CONCEPT 31.2

Fungi produce spores through sexual or asexual life cycles

Most fungi propagate themselves by producing vast numbers of spores, either sexually or asexually. For example, puffballs, the reproductive structures of certain fungal species, may release trillions of spores (see Figure 31.17). Spores can be carried long distances by wind or water. If they land in a moist place where there is food, they germinate, producing a new mycelium. To appreciate how effective spores are at dispersing, leave a slice of melon exposed to the air. Even without a visible source of spores nearby, within a week, you will likely observe fuzzy mycelia growing from microscopic spores that have fallen onto the melon.

▼ **Figure 31.5 Generalized life cycle of fungi.** Many fungi reproduce both sexually and asexually, as shown here; others, however, reproduce only sexually or asexually.



? *Compare the genetic variation found in spores produced in the sexual and asexual portions of the life cycle. Why do these differences occur?*

Figure 31.5 generalizes the many different life cycles that can produce fungal spores. In this section, we will survey the main aspects of sexual and asexual reproduction in fungi.

Sexual Reproduction

The nuclei of fungal hyphae and the spores of most fungi are haploid, although many species have transient diploid stages that form during sexual life cycles. Sexual reproduction often begins when hyphae from two mycelia release signaling molecules called **pheromones**. If the mycelia are of different mating types, the pheromones from each partner bind to receptors on the other, and the hyphae extend toward the source of the pheromones. When the hyphae meet, they fuse. In species with such a "compatibility test," this process contributes to genetic variation by preventing hyphae from fusing with other hyphae from the same mycelium or another genetically identical mycelium.

The union of the cytoplasms of two parent mycelia is known as **plasmogamy** (see Figure 31.5). In most fungi, the haploid nuclei contributed by each parent do not fuse right away. Instead, parts of the fused mycelium contain coexisting, genetically different nuclei. Such a mycelium is said to be a **heterokaryon** (meaning "different nuclei"). In some species, the haploid nuclei pair off two to a cell, one from each parent. Such a mycelium is **dikaryotic** (meaning "two nuclei"). As a dikaryotic mycelium grows, the two nuclei in each cell divide in tandem without fusing. Because these cells retain two separate haploid nuclei, they differ from diploid cells, which have pairs of homologous chromosomes within a single nucleus.

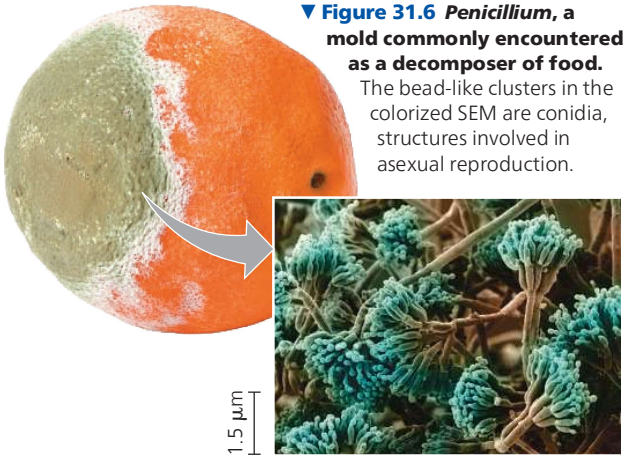
Hours, days, or (in some fungi) even centuries may pass between plasmogamy and the next stage in the sexual cycle, **karyogamy**. During karyogamy, the haploid nuclei contributed by the two parents fuse, producing diploid cells. Zygotes and other transient structures form during karyogamy, the only diploid stage in most fungi. Meiosis then restores the haploid condition, ultimately leading to the formation of genetically diverse spores. Meiosis is a key step in sexual reproduction, so spores produced in this way are sometimes referred to as "sexual spores."

The sexual processes of karyogamy and meiosis generate extensive genetic variation, a prerequisite for natural selection. (See Concepts 13.2 and 23.1 to review how sex can increase genetic diversity.) The heterokaryotic condition also offers some of the advantages of diploidy in that one haploid genome may compensate for harmful mutations in the other.

Asexual Reproduction

Many fungi reproduce both sexually and asexually, as shown in Figure 31.5; others, however, reproduce only sexually or only asexually. As with sexual reproduction, the processes of asexual reproduction vary widely among fungi.

Many fungi reproduce asexually by growing as filamentous fungi that produce (haploid) spores by mitosis; such species are informally referred to as **molds** if they form visible mycelia. Depending on your housekeeping habits, you may have observed molds in your kitchen, forming furry carpets on bread or fruit **(Figure 31.6)**. Molds typically grow rapidly and produce many spores asexually, enabling the fungi to colonize new sources of food. Many species that

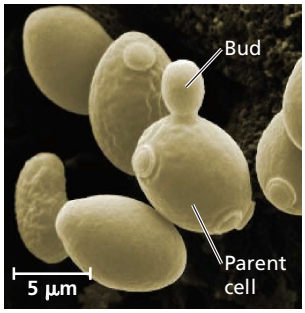


▼ **Figure 31.6 *Penicillium*, a mold commonly encountered as a decomposer of food.** The bead-like clusters in the colorized SEM are conidia, structures involved in asexual reproduction.

produce such spores can also reproduce sexually if they happen to contact a member of their species of a different mating type.

Other fungi reproduce asexually by growing as single-celled yeasts. Instead of producing spores, asexual reproduction in yeasts occurs by ordinary cell division or by the pinching of small "bud cells" off a parent cell **(Figure 31.7)**. As already mentioned, some fungi that grow as yeasts can also grow as filamentous mycelia.

▼ Figure 31.7 The yeast *Saccharomyces cerevisiae* in stages of budding. (SEM)



Many yeasts and filamentous fungi have no known sexual stage in their life cycle. Since early mycologists (biologists who study fungi) classified fungi based mainly on their type of sexual structure, this posed a problem. Mycologists have traditionally lumped all fungi lacking sexual reproduction into a group called **deuteromycetes** (from the Greek *deutero*, second, and *mycete*, fungus). Whenever a sexual stage is discovered for a so-called deuteromycete, the species is reclassified in a particular phylum, depending on the type of sexual structures it forms. In addition to searching for sexual stages of such unassigned fungi, mycologists can now use genomic techniques to classify them.

CONCEPT CHECK 31.2

1. **MAKE CONNECTIONS** Compare Figure 31.5 with Figure 13.6. In terms of haploidy versus diploidy, how do the life cycles of fungi and humans differ?
2. **WHAT IF?** Suppose that you sample the DNA of two mushrooms on opposite sides of your yard and find that they are identical. Propose two hypotheses that could reasonably account for this result.

For suggested answers, see Appendix A.

CONCEPT 31.3

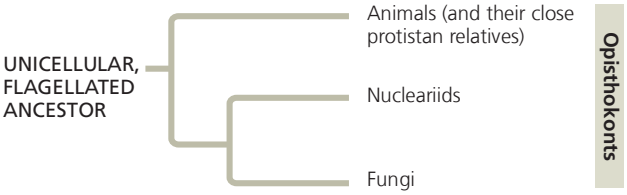
The ancestor of fungi was an aquatic, single-celled, flagellated protist

Data from molecular systematics offer insights into the early evolution of fungi. As a result, systematists now recognize that fungi and animals are more closely related to each other than either group is to plants or to most other eukaryotes.

The Origin of Fungi

Phylogenetic analyses suggest that fungi evolved from a flagellated ancestor. While the majority of fungi lack flagella, two basal lineages of fungi (the cryptomycetes and the chytrids, as we'll discuss shortly) do have flagella. Moreover, most of

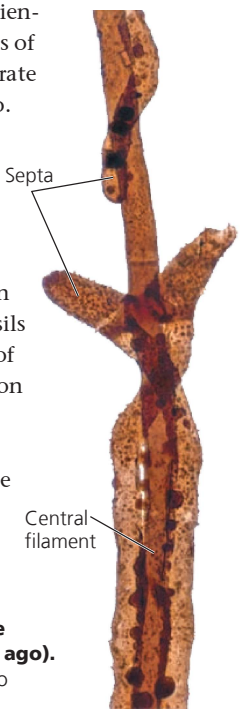
▼ Figure 31.8 Fungi and their close relatives. Molecular evidence indicates that the nucleariids, a group of single-celled protists, are the closest living relatives of fungi.



the protists that share a close common ancestor with animals and fungi also have flagella. DNA sequence data indicate that these three groups of eukaryotes—the fungi, the animals, and their protistan relatives—form a monophyletic group, or clade **(Figure 31.8)**. As discussed in Concept 28.5, members of this clade are called **opisthokonts**, a name that refers to the posterior (*opistho-*) location of the flagellum in these organisms.

Within the opisthokont clade, fungi are more closely related to several groups of single-celled protists than they are to animals, suggesting that the ancestor of fungi was unicellular. One such group of unicellular protists, the **nucleariids**, consists of amoebas that feed on algae and bacteria. DNA evidence further indicates that animals are more closely related to a *different* group of protists (the choanoflagellates) than they are to either fungi or nucleariids. Together, these results suggest that multicellularity evolved in animals and fungi independently, from different single-celled ancestors.

Using molecular clock analyses, scientists have estimated that the ancestors of animals and fungi diverged into separate lineages more than a billion years ago. Fossils of certain unicellular, marine eukaryotes that lived as early as 1.5 billion years ago have been interpreted as fungi, but those claims remain controversial. Furthermore, although fungi probably originated in aquatic environments, the oldest fossils that are widely accepted as fungi are of terrestrial species that lived 440 million years ago **(Figure 31.9)**. Fungi may have colonized land as early as 505 million years ago: Soils of that age



▶ Figure 31.9 Fossil hyphae from the fungus *Tortotubus* (440 million years ago). The central filament is surrounded by two partially overlapping filaments (LM).

have a chemical "signature" similar to that found in soils where fungi are active today. Overall, more fossils are needed to help clarify when fungi originated and what features were present in their earliest lineages.

The Move to Land

Plants colonized land about 470 million years ago (see Concept 29.1), and fungi may well have colonized land before plants. Indeed, some researchers have described life on land before the arrival of plants as a "green slime" that consisted of cyanobacteria, algae, and a variety of small, heterotrophic species, including fungi. With their capacity for extracellular digestion, fungi would have been well suited for feeding on other early terrestrial organisms (or their remains).

Once on land, some fungi formed symbiotic associations with early plants. For example, 405-million-year-old fossils of the early plant *Aglaophyton* contain evidence of mycorrhizal relationships between plants and fungi (see Figure 25.13). This evidence includes fossils of hyphae that have penetrated within plant cells and formed structures that resemble the arbuscules formed today by arbuscular mycorrhizae. Similar structures have been found in a variety of other early plants, suggesting that plants probably existed in beneficial relationships with fungi from the earliest periods of colonization of land. The earliest plants lacked roots, limiting their ability to extract nutrients from the soil. As occurs in mycorrhizal associations today, it is likely that soil nutrients were transferred to early plants via the extensive mycelia formed by their symbiotic fungal partners.

Support for the antiquity of mycorrhizal associations has also come from molecular studies. For a mycorrhizal fungus and its plant partner to establish a symbiotic relationship, certain genes must be expressed by the fungus and other genes must be expressed by the plant. Researchers focused on three plant genes (called *sym* genes) whose expression is required for the formation of mycorrhizae in flowering plants. They found that these genes were present in all major plant lineages, including basal lineages such as liverworts (see Figure 29.13). Furthermore, after they transferred a liverwort *sym* gene to a flowering plant mutant that could not form mycorrhizae, the mutant recovered its ability to form mycorrhizae. These results suggest that mycorrhizal *sym* genes were present in early plants—and that the function of these genes has been conserved for hundreds of millions of years as plants continued to adapt to life on land.

CONCEPT CHECK 31.3

1. Why are fungi classified as opisthokonts despite the fact that most fungi lack flagella?
2. Describe the importance of mycorrhizae, both today and in the colonization of land. What evidence supports the antiquity of mycorrhizal associations?
3. **WHAT IF?** If fungi colonized land before plants, where might the fungi have lived? How would their food sources have differed from what they feed on today?

For suggested answers, see Appendix A.

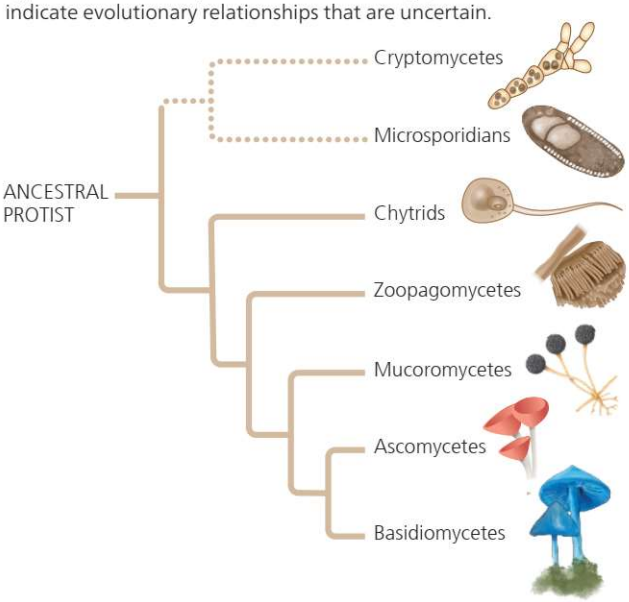
CONCEPT 31.4

Fungi have radiated into a diverse set of lineages

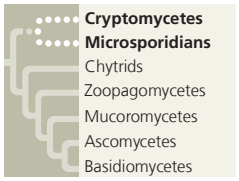
In the past decade, molecular analyses have reshaped our understanding of the evolutionary relationships between fungal groups. In addition, metagenomic studies have led to the discovery of entirely new groups of fungi. As a result, the phylogeny of fungi is undergoing dramatic change. For example, one traditional group, the Zygomycota, has been abandoned because it was paraphyletic, and its members have been reassigned to other groups. Recent studies also indicate that the *microsporidians*, an enigmatic group of unicellular parasites, should be classified as fungi and may belong to a basal fungal lineage (one that diverged from other fungi early in the history of the group).

Figure 31.10 presents a current hypothesis of the relationships among fungal groups. In this section, we'll survey the groups identified in this phylogenetic tree. However, the groups shown in Figure 31.10 may represent only a small fraction of the diversity of extant fungal groups. (Extant lineages are those that have surviving members.) While there are about 145,000 known species of fungi, in recent years more than 2,000 new species have been discovered annually. By some estimates the actual number of fungal species lies between 2.2 and 3.8 million—more than all of the 1.9 million species of organisms (of every type) that biologists have currently identified and named.

▼ Figure 31.10 Phylogeny of fungi. This phylogenetic hypothesis shows major clades of extant fungi; dotted lines indicate evolutionary relationships that are uncertain.



Cryptomycetes and Microsporidians



Genomic studies indicate that **cryptomycetes** (fungi in the phylum Cryptomycota) and **microsporidians** (fungi in the phylum Microsporidia) form a sister group and are a basal fungal lineage (see Figure 31.10). While most molecular comparisons support the placement of cryptomycetes and microsporidians at the base of the fungal tree, more data are needed to help resolve this phylogeny.

Cryptomycetes

Although only 30 species have been identified to date, genetic data suggest that the cryptomycetes are a large and diverse group. DNA sequences from members of this group have been found in marine and freshwater communities, as well as soils. Cryptomycetes also have been found in aerobic and anaerobic environments, and in geographical locations across the globe. Like the species shown in **Figure 31.11**, *Rozella allomycis*, many of the cryptomycetes identified to date are parasites of protists and other fungi.

▼ Figure 31.11 The cryptomycete *Rozella allomycis* parasitizing another fungus.



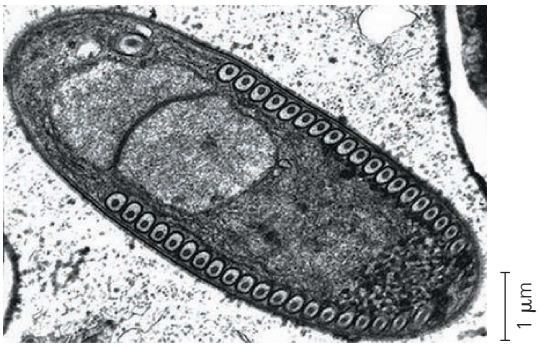
Cryptomycetes are unicellular and have flagellated spores. Cryptomycetes also can synthesize a chitin-rich cell wall, a key structural feature of the fungi (see Concept 31.1).

Microsporidians

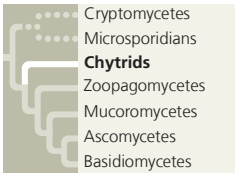
The 1,300 species of microsporidians are unicellular parasites of protists and animals, including humans **(Figure 31.12)**. Infections in humans can cause reduced longevity and weight loss. The microsporidian *Nosema ceranae* is a parasite of honeybees and may contribute to *Colony Collapse Disorder*, a devastating outbreak that has led to the loss of honeybee colonies throughout the world.

Like all fungi, microsporidians can synthesize a chitin-rich cell wall. Other aspects of their biology are unusual. For example, microsporidians have highly reduced mitochondria and small genomes, with only 2,000 genes in some species. The genome of one microsporidian, *Encephalitozoon intestinalis*, has just 2.3 Mb of DNA—the smallest genome of any eukaryote sequenced to date. Unlike other basal fungi, microsporidians lack flagellated spores; instead, they produce unique spores that infect host cells via a harpoon-like organelle.

▼ Figure 31.12 A spore of the microsporidian *Fibrillanosema crangonycis*. (TEM)



Chytrids

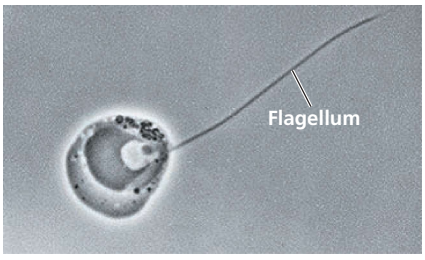


The fungi classified in phylum Chytridiomycota, called **chytrids**, are ubiquitous in lakes and soil; recent metagenomic studies have uncovered new clades of chytrids in hydrothermal vent and other marine communities. Some of the approximately 1,000 chytrid species are decomposers, while others are parasites of protists, other fungi, plants, or animals; as we'll see later in the chapter, two chytrid parasites have contributed to the global decline of amphibian populations. Still other chytrids are important mutualists. For example, anaerobic chytrids that live in the digestive tracts of sheep and cattle help to break down plant matter, thereby contributing significantly to the animal's growth.

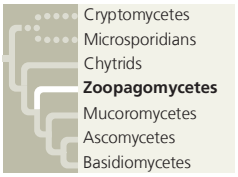
Nearly all chytrids have flagellated spores, called **zoospores (Figure 31.13)**. Like other fungi, chytrids have cell walls made of chitin, and they also share certain key enzymes and metabolic pathways with other fungal groups. Some chytrids form colonies with hyphae, while others exist as single spherical cells.

Mastering Biology Video: *Phlyctochytrium* Zoospore Release

▶ Figure 31.13 Flagellated chytrid zoospore. (TEM)



Zoopagomycetes



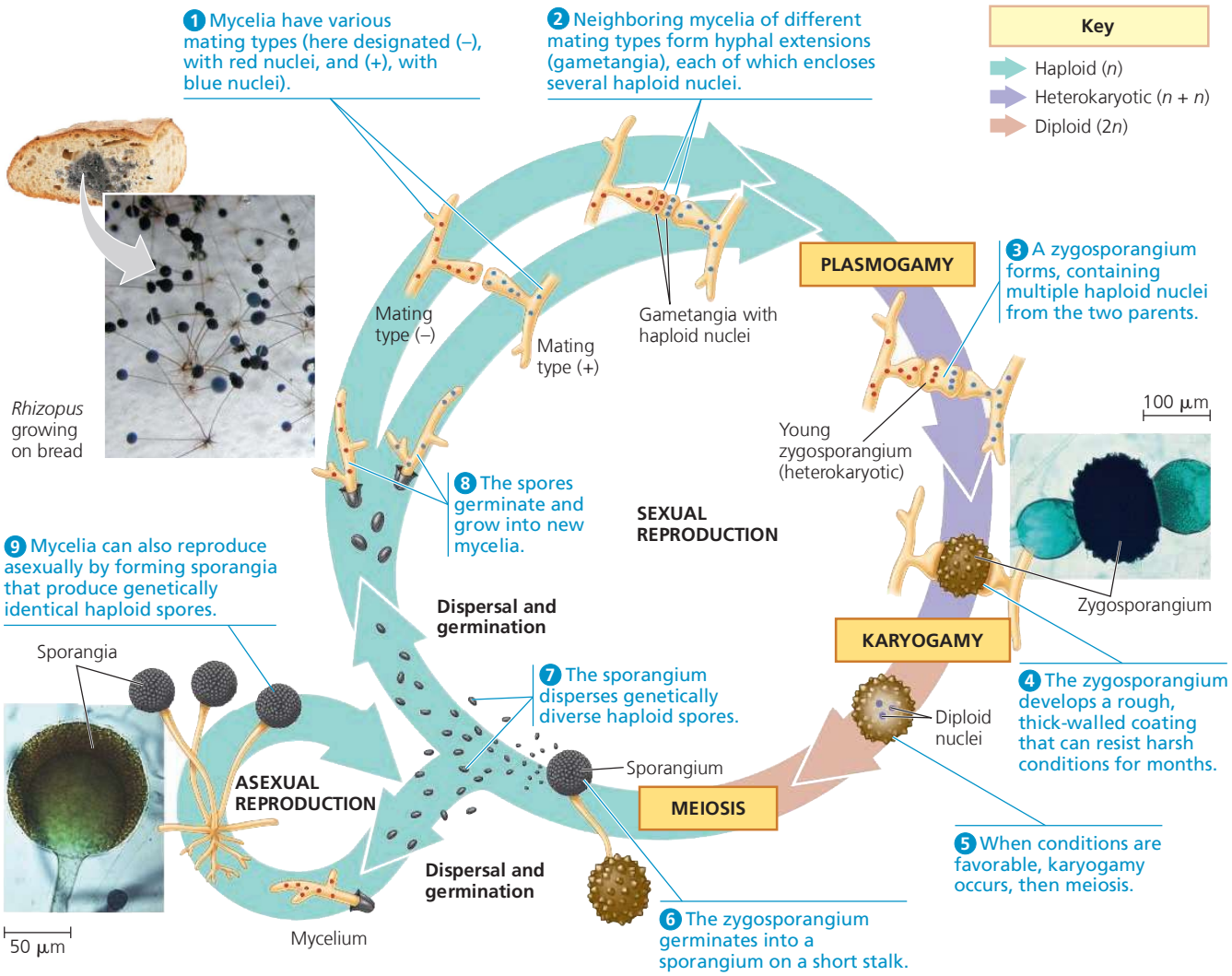
Most of the 900 species of **zoopagomycetes**, fungi in the phylum Zoopagomycota, live as parasites or as commensal (neutral) symbionts of animals; some are parasites of other fungi or protists. Zoopagomycetes form filamentous hyphae and reproduce asexually by producing nonflagellated spores. Some zoopagomycetes induce insects that they parasitize to perch near the top of plants; the insects subsequently die and fungal spores are released to infect new victims **(Figure 31.14)**. Sexual reproduction, where known, involves the formation of a durable structure called a zygosporangium, which houses and protects the zygote.

The loss of flagellated spores in the zoopagomycetes and other fungal lineages may have been associated with a transition to life on land. Basal fungal lineages had flagellated spores, enabling dispersal through water. In contrast, zoopagomycetes and all of their closest fungal relatives (the clade consisting of the mucoromycetes, ascomycetes, and



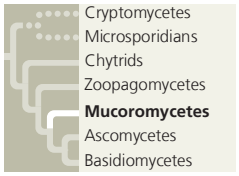
◀ Figure 31.14 A fly covered with fungal hyphae. This fly was killed by the zoopagomycete *Entomophthora muscae*, also known as the "fly death fungus," for obvious reasons.

▼ Figure 31.15 The life cycle of the mucoromycete *Rhizopus stolonifer* (black bread mold).



basidiomycetes; see Figure 31.10) have nonflagellated spores, which are dispersed by wind in terrestrial fungi.

Mucoromycetes



There are approximately 750 known species of **mucoromycetes**, fungi in the phylum Mucoromycota. This phylum includes species of fast-growing molds responsible for causing foods such as bread, peaches, strawberries, and sweet potatoes to rot during storage. Although some mucoromycetes are decomposers, most are associated with plants. Many mucoromycetes live as parasites or pathogens of plants, while others live as mutualists (including some mycorrhizae).

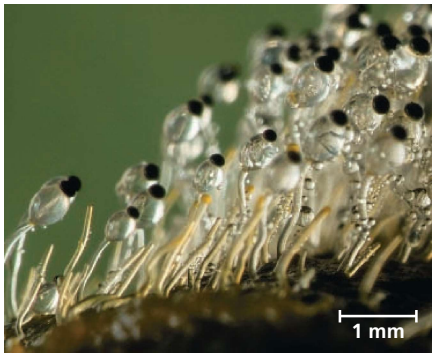
The life cycle of *Rhizopus stolonifer* (black bread mold) is fairly typical of mucoromycete species **(Figure 31.15)**. Its hyphae spread out over the food surface, penetrate it, and absorb nutrients. The hyphae are coenocytic, with septa found only where reproductive cells are formed. In the asexual phase, bulbous black sporangia develop at the tips of upright hyphae. Within each sporangium, hundreds of genetically identical haploid spores develop and are dispersed through the air. Spores that happen to land on moist food germinate, growing into new mycelia.

If environmental conditions deteriorate—for instance, if the mold consumes all its food—*Rhizopus* may reproduce sexually. The parents in a sexual union are mycelia of different mating types, which possess different chemical markers but may appear identical. Plasmogamy produces a sturdy structure called a **zygosporangium** (plural, *zygosporangia*), in which karyogamy and then meiosis occur. Note that while a zygosporangium represents the zygote ($2n$) stage in the life cycle, it is not a zygote in the usual sense (that is, a cell with one diploid nucleus). Rather, a zygosporangium is a multinucleate structure, first heterokaryotic with many haploid nuclei from the two parents, then with many diploid nuclei after karyogamy.

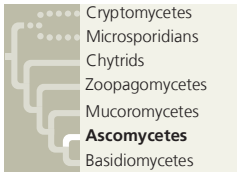
Zygosporangia are resistant to freezing and drying and are metabolically inactive. When conditions improve, the nuclei of the zygosporangium undergo meiosis, the zygosporangium germinates into a sporangium, and the sporangium releases genetically diverse haploid spores that may colonize a new substrate. Some mucoromycetes can actually "aim" and then shoot their sporangia toward bright light. **Figure 31.16** shows one example, *Pilobolus*, which decomposes animal dung. Its sporebearing hyphae bend toward light, where there are likely to be openings in the vegetation through which spores may reach fresh grass. The fungus then launches its sporangia in a jet of water that can travel up to 2.5 m. Grazing animals ingest the fungi with the grass and then scatter the spores in feces, thereby enabling the next generation of fungi to grow.

Finally, the phylum Mucoromycota also includes the glomeromycetes, a clade of fungi that form arbuscular mycorrhizae (see Figure 31.4b and Figure 37.14). The tips of the hyphae that push into plant root cells branch into tiny treelike arbuscules. About 85% of all plant species have mutualistic partnerships with arbuscular mycorrhizae.

▶ Figure 31.16 *Pilobolus* aiming its sporangia.



Ascomycetes



Mycologists have described 90,000 species of **ascomycetes**, fungi in the phylum Ascomycota, from a wide variety of marine, freshwater, and terrestrial habitats. The defining feature of ascomycetes is the production of spores (called ascospores) in saclike **asci** (singular, *ascus*); thus, they are commonly called *sac fungi*. During their sexual stage, most ascomycetes develop fruiting bodies, called **ascocarps**, which range in size from microscopic to macroscopic **(Figure 31.17)**. The ascocarps contain the spore-forming asci.

Ascomycetes vary in size and complexity from unicellular yeasts to elaborate cup fungi and morels (see Figure 31.17). They include some of the most devastating plant pathogens, which we will discuss later. However, many ascomycetes are important decomposers, particularly of plant material. More than 25% of all ascomycete species live with green algae or cyanobacteria in beneficial symbiotic associations called lichens. Some ascomycetes form mycorrhizae with plants.

▼ Figure 31.17 Ascomycetes (sac fungi).



▶ *Tuber melanosporum* is a truffle species that forms ectomycorrhizae with trees. The ascocarp grows underground and emits a strong odor. These ascocarps have been dug up and the middle one sliced open.



◀ The edible ascocarp of *Morchella esculenta*, the tasty morel, is often found under trees in orchards.

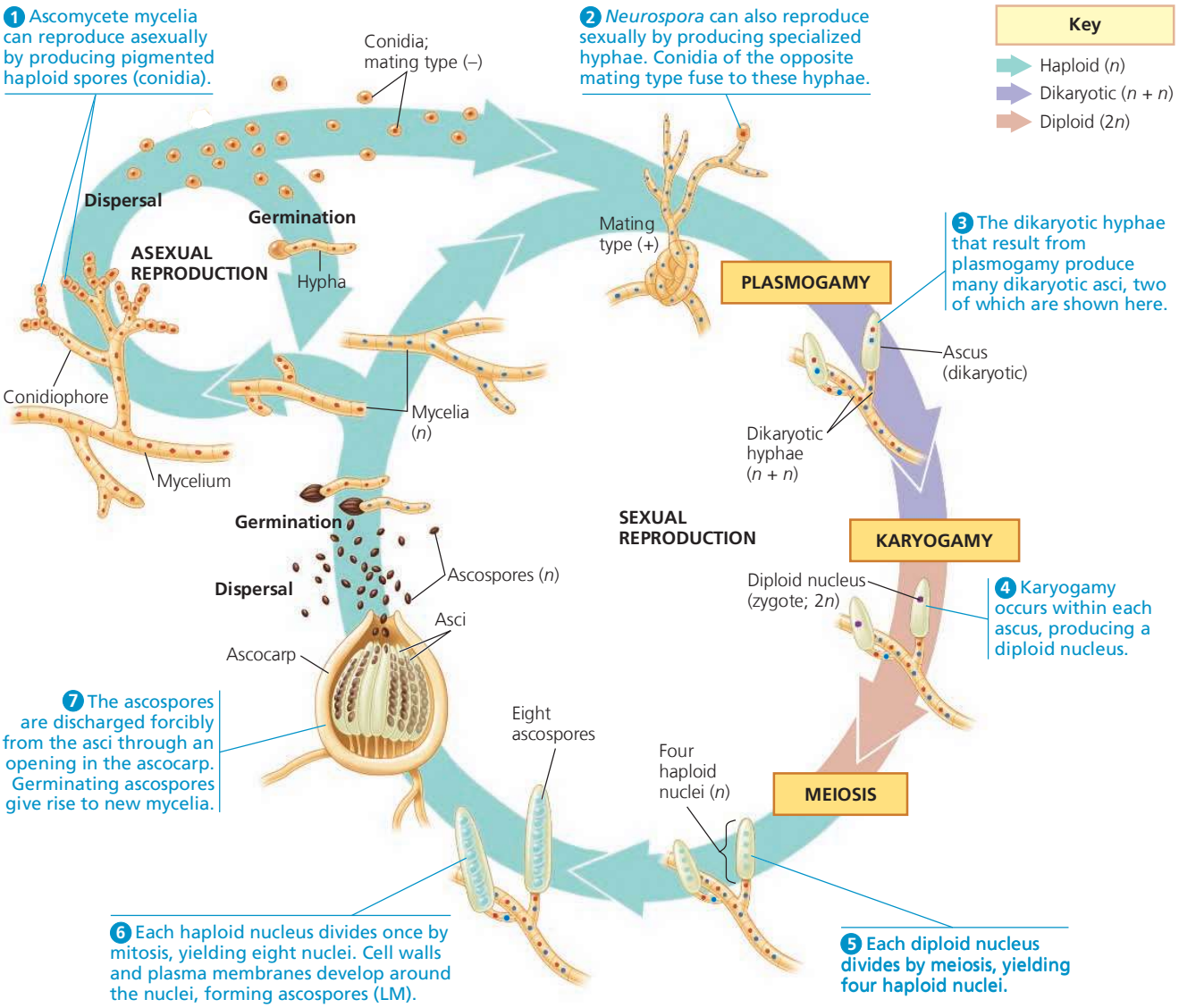
? *Ascomycetes vary greatly in morphology (see also Figure 31.10). How could you confirm that a fungus is an ascomycete?*

Many others live between mesophyll cells in leaves; some of these species release toxic compounds that help protect the plant from insects.

Although the life cycles of various ascomycete groups differ in the details of their reproductive structures and processes, we'll illustrate some common elements using the bread mold *Neurospora crassa* **(Figure 31.18)**. Ascomycetes reproduce asexually by producing enormous numbers of asexual spores called **conidia** (singular, *conidium*). Unlike the asexual spores of most mucoromycetes, in most ascomycetes, conidia are not formed inside sporangia. Rather, they are produced externally at the tips of specialized hyphae called conidiophores, often in clusters or long chains, from which they may be dispersed by the wind.

Conidia may also be involved in sexual reproduction, fusing with hyphae from a mycelium of a different mating type, as occurs in *Neurospora*. Fusion of two different mating types is followed by plasmogamy, resulting in the formation of dikaryotic cells, each with two haploid nuclei representing the two parents. The cells at the tips of these dikaryotic hyphae develop into many asci. Within each ascus, karyogamy combines the two parental genomes, and then meiosis forms four genetically different nuclei. This is usually followed by a mitotic division, forming eight ascospores. The

▼ Figure 31.18 The life cycle of *Neurospora crassa*, an ascomycete. *Neurospora* is a bread mold and research organism that also grows in the wild on burned vegetation.



VISUAL SKILLS *What is the ploidy of a cell in the specialized hypha shown in* 2*?*

ascospores develop in and are eventually discharged from the ascocarp.

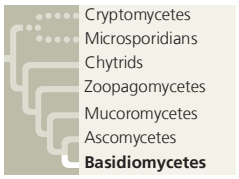
Compared to the life cycle of mucoromycetes, the extended dikaryotic stage of ascomycetes (and also basidiomycetes) provides additional opportunities for genetic recombination. In *Neurospora*, for example, many dikaryotic cells can develop into asci. The haploid nuclei in these asci fuse, and their genomes then recombine during meiosis, resulting in a multitude of genetically different offspring from one mating event (see steps 3–5 in Figure 31.18).

As described in Figure 17.2, biologists in the 1930s used *Neurospora* in research that led to the one gene–one enzyme hypothesis. Today, this ascomycete continues to serve as a model research organism. In 2003, its entire genome was published. This tiny fungus has about three-fourths as many genes as the fruit fly *Drosophila* and about half as many as a human **(Table 31.1)**. The *Neurospora* genome is relatively compact, having few of the stretches of noncoding DNA that occupy so much space in the genomes of humans and many other eukaryotes. In fact, there is evidence that *Neurospora* has a genomic defense system that prevents noncoding DNA such as transposons from accumulating.

Table 31.1 Comparison of Gene Density in *Neurospora*, *Drosophila*, and *Homo sapiens*

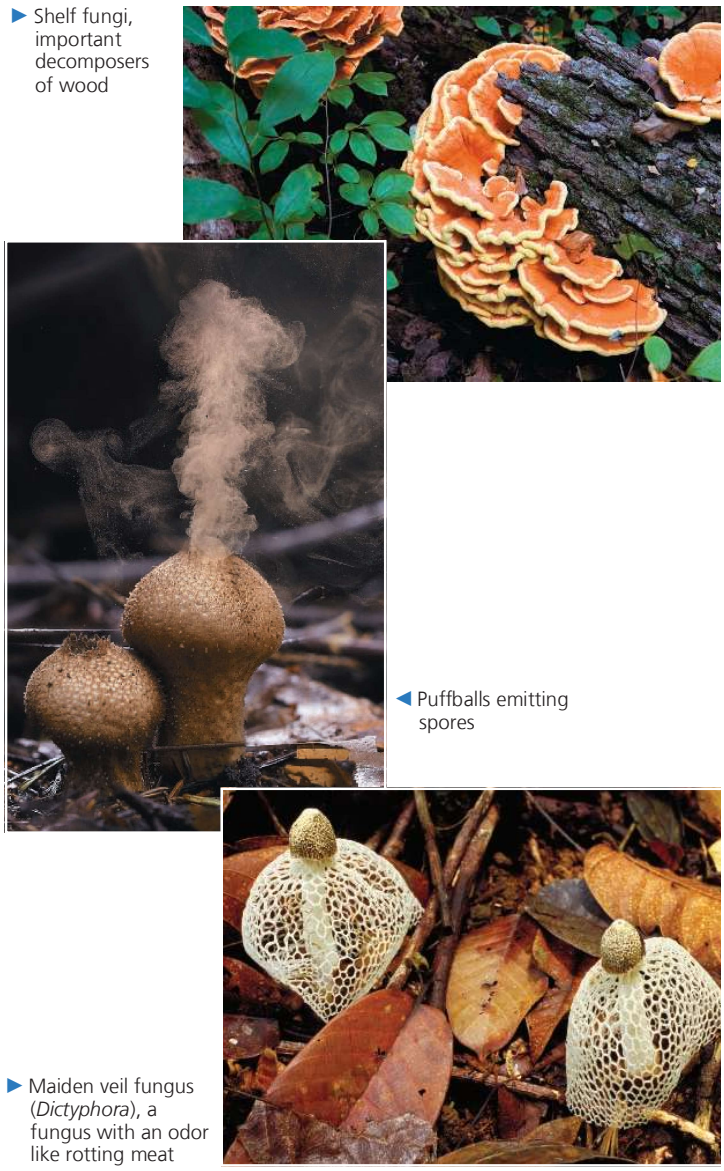
	Genome Size (million base pairs)	Number of Genes	Gene Density (genes per million base pairs)
Neurospora crassa (ascomycete fungus)	41	9,700	236
Drosophila melanogaster (fruit fly)	165	14,000	85
Homo sapiens (human)	3,000	<21,000	7

Basidiomycetes



About 50,000 species, including mushrooms, puffballs, and shelf fungi, are called **basidiomycetes** and are classified in the phylum Basidiomycota **(Figure 31.19)**. This phylum also includes mutualists that form mycorrhizae and two groups of destructive plant parasites: rusts and smuts. The name of the phylum derives from the **basidium** (plural, *basidia*; Latin for "little pedestals"), a cell in which karyogamy occurs, followed immediately by meiosis. The club-like shape of the basidium also gives rise to the common name *club fungus*.

▼ Figure 31.19 Basidiomycetes (club fungi).



▶ Shelf fungi, important decomposers of wood

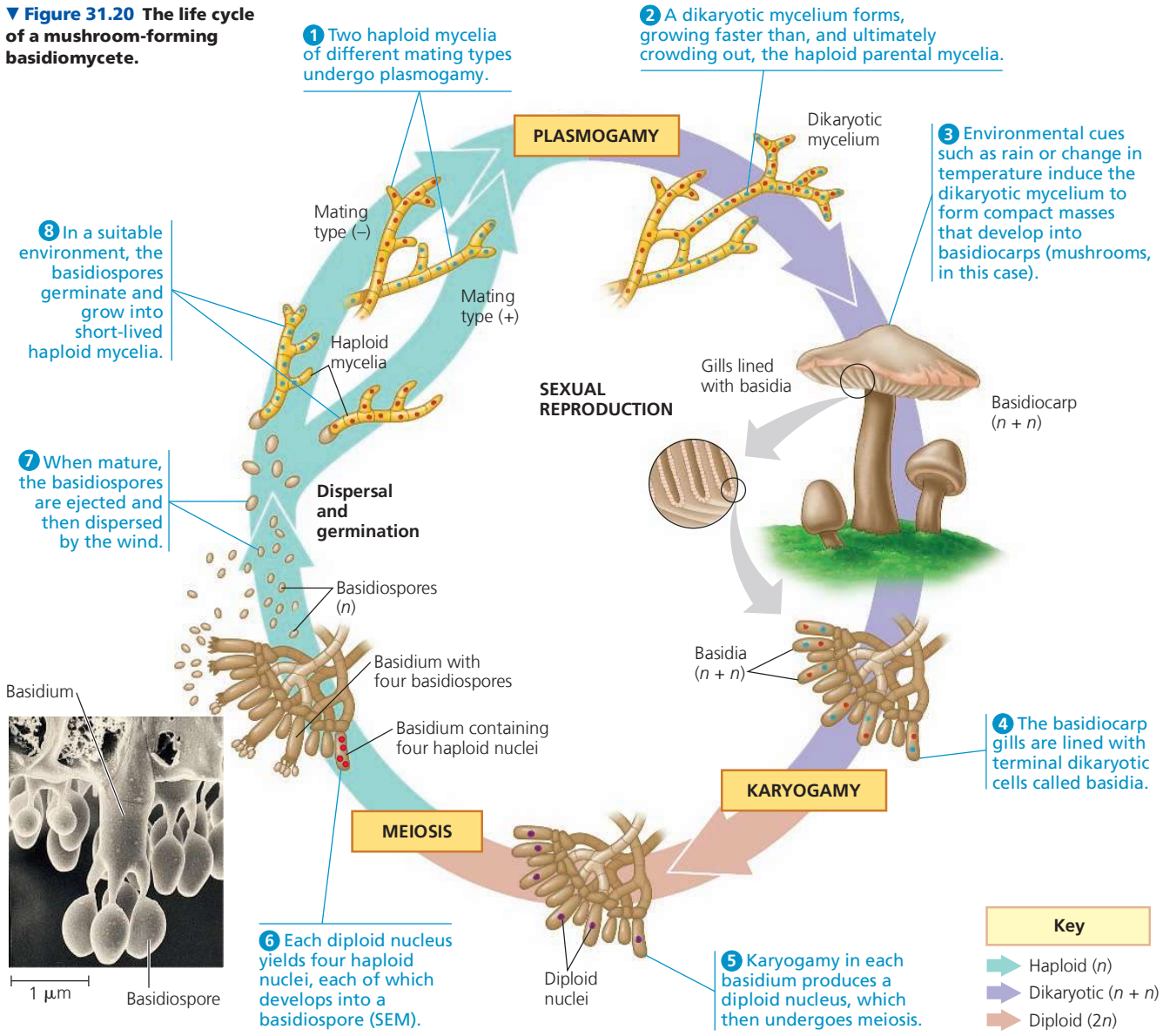
◀ Puffballs emitting spores

▶ Maiden veil fungus (*Dictyphora*), a fungus with an odor like rotting meat

Basidiomycetes are important decomposers of wood and other plant material. Of all the fungi, certain basidiomycetes are the best at decomposing the complex polymer lignin, an abundant component of wood. Many shelf fungi break down the wood of weak or damaged trees and continue to decompose the wood after the tree dies.

The life cycle of a basidiomycete usually includes a long-lived dikaryotic mycelium. As in ascomycetes, this extended dikaryotic stage provides many opportunities for genetic recombination events, in effect multiplying the result of a single mating. Periodically, in response to environmental stimuli, the mycelium reproduces sexually by producing

▼ Figure 31.20 The life cycle of a mushroom-forming basidiomycete.



VISUAL SKILLS *Use the diagram to determine the ploidy of a cell in the aboveground stalk of a mushroom.*

Mastering Biology **Animation: Life Cycle of a Mushroom**

elaborate fruiting bodies called **basidiocarps (Figure 31.20)**. The common white mushrooms in the supermarket are familiar examples of a basidiocarp.

By concentrating growth in the hyphae of mushrooms, a basidiomycete mycelium can erect its fruiting structures in just a few hours; a mushroom pops up as it absorbs water and as cytoplasm streams in from the dikaryotic mycelium. By this process, in some species a ring of mushrooms, popularly called a "fairy ring," may appear literally overnight **(Figure 31.21)**. The mycelium below the fairy ring expands outward at a rate of about 30 cm per year, decomposing organic matter in the soil as it grows. Some giant fairy rings are produced by mycelia that are centuries old.

After a mushroom forms, its cap supports and protects a large surface area of dikaryotic basidia on gills. During karyogamy, the two nuclei in each basidium fuse, producing a diploid nucleus (see Figure 31.20). This nucleus then undergoes meiosis, yielding four haploid nuclei, each of which ultimately develops into a basidiospore. Large numbers of basidiospores are produced: The gills of a common white mushroom have a surface area of about 200 cm^2 and may drop a billion basidiospores, which blow away.

▼ **Figure 31.21 A fairy ring.** According to legend, mushroom rings spring up where fairies have danced on a moonlit night. The text provides a biological explanation of how these rings form.



CONCEPT CHECK 31.4

1. What feature of chytrids supports the hypothesis that they include members of basal fungal lineages?
2. Give examples of how form fits function in mucoromycetes, ascomycetes, and basidiomycetes.
3. **WHAT IF?** Suppose that the mutation of an ascomycete changed its life cycle so that plasmogamy, karyogamy, and meiosis occurred in quick succession. How might this affect the ascospores and ascocarps?

For suggested answers, see Appendix A.

CONCEPT 31.5

Fungi play key roles in nutrient cycling, ecological interactions, and human welfare

In our survey of fungal classification, we've touched on some of the ways fungi influence other organisms. We will now look more closely at these impacts, focusing on how fungi act as decomposers, mutualists, and pathogens.

Fungi as Decomposers

Fungi are well adapted as decomposers of organic material, including the cellulose and lignin of plant cell walls. In fact, almost any carbon-containing substrate—even jet fuel and house paint—can be consumed by at least some fungi. The same is true of bacteria. As a result, fungi and bacteria are primarily responsible for keeping ecosystems stocked with the inorganic nutrients essential for plant growth. Without these decomposers, carbon, nitrogen, and other elements would remain tied up in organic matter. If that were to happen, plants and the animals that eat them could not exist because elements taken from the soil would not be returned. Without decomposers, life as we know it would cease.

Fungi as Mutualists

Fungi may form mutualistic relationships with plants, algae, cyanobacteria, and animals. Mutualistic fungi absorb nutrients from a host organism, but they reciprocate with actions that benefit the host—as we already saw for the key mycorrhizal associations that fungi form with most vascular plants. We turn now to other examples of mutualistic fungi.

Fungus-Plant Mutualisms

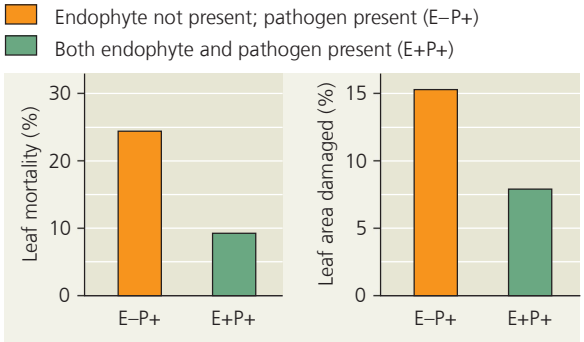
All plant species studied to date appear to harbor symbiotic **endophytes**, fungi (or bacteria) that live inside leaves or other plant parts without causing harm. Most fungal endophytes identified to date are ascomycetes but some are mucoromycetes. Fungal endophytes benefit certain grasses and other nonwoody plants by making toxins that deter herbivores or by increasing host plant tolerance of heat, drought, or heavy metals. As described in **Figure 31.22**, researchers

▼ **Figure 31.22 Inquiry**

Do fungal endophytes benefit a woody plant?

Experiment Fungal endophytes are symbiotic fungi found within the bodies of all plants examined to date. Researchers tested whether fungal endophytes benefit the cacao tree (*Theobroma cacao*). This tree, whose name means "food of the gods" in Greek, is the source of the beans used to make chocolate, and it is cultivated throughout the tropics. A particular mixture of fungal endophytes was added to the leaves of some cacao seedlings, but not others. (In cacao, fungal endophytes colonize leaves after the seedling germinates.) The seedlings were then inoculated with a virulent pathogen, the protist *Phytophthora*.

Results Fewer leaves were killed by the pathogen in seedlings with fungal endophytes than in seedlings without endophytes. Among leaves that survived, pathogens damaged less of the leaf surface area in seedlings with endophytes than in seedlings without endophytes.



Conclusion The presence of endophytes appears to benefit cacao trees by reducing the leaf mortality and damage caused by *Phytophthora*.

Data from A. E. Arnold et al., Fungal endophytes limit pathogen damage in a tropical tree, *Proceedings of the National Academy of Sciences USA* 100:15649–15654 (2003).

WHAT IF? *The researchers also performed control treatments. Suggest two controls they might have used, and explain how each would be helpful in interpreting the results described here.*

▼ Figure 31.23 Fungus-gardening insects. These leaf-cutting ants depend on fungi to convert plant material to a form the insects can digest. The fungi, in turn, depend on the nutrients from the leaves the ants feed them.



studying how fungal endophytes affect a woody plant tested whether leaf endophytes benefit seedlings of the cacao tree, *Theobroma cacao*. Their findings show that the fungal endophytes of woody flowering plants can play an important role in defending against pathogens.

Fungus-Animal Mutualisms

As mentioned earlier, some fungi share their digestive services with animals, helping break down plant material in the guts of cattle and other grazing mammals. Many species of ants take advantage of the digestive power of fungi by raising them in "farms." Leaf-cutter ants, for example, scour tropical forests in search of leaves, which they cannot digest on their own but carry back to their nests and feed to the fungi **(Figure 31.23)**. As the fungi grow, their hyphae develop specialized swollen tips that are rich in proteins and carbohydrates. The ants feed primarily on these nutrient-rich tips. Not only do the fungi break down plant leaves into substances the insects can digest, but they also detoxify plant defensive compounds that would otherwise kill or harm the ants. In some tropical forests, the fungi have helped these insects become the major consumers of leaves.

The evolution of such farmer ants and that of their fungal "crops" have been tightly linked for over 50 million years. The fungi have become so dependent on their caretakers that in many cases they can no longer survive without the ants, and vice versa.

Lichens

A **lichen** is a symbiotic association between a photosynthetic microorganism and a fungus in which millions of photosynthetic cells are held in a mass of fungal hyphae. Lichens grow on the surfaces of rocks, rotting logs, trees, and roofs in various forms **(Figure 31.24)**. The photosynthetic partners are unicellular or filamentous green algae or cyanobacteria. The fungal component is most often an ascomycete, but some

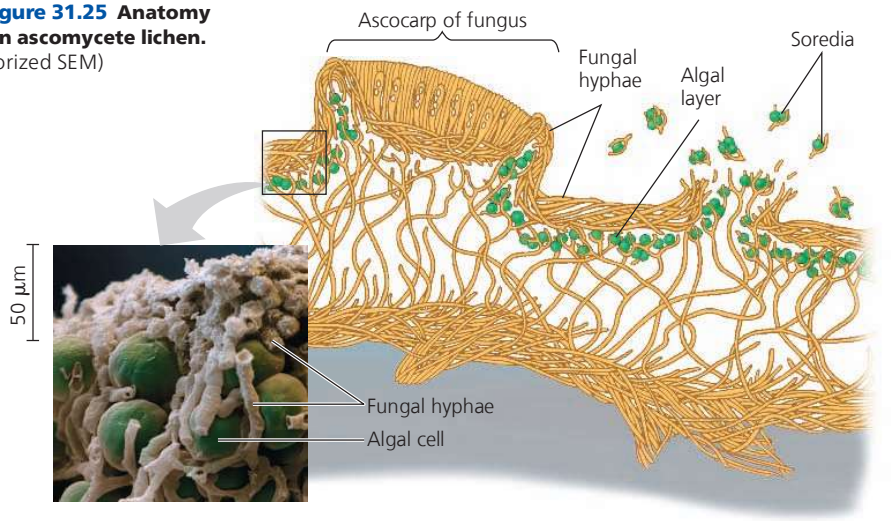
▼ Figure 31.24 Variation in lichen growth forms.



glomeromycete and basidiomycete lichens are known. Recent studies have found that many lichens also have a basidiomycete yeast as a second fungal component. As the role of these yeasts remains unknown, our discussion will focus on the primary fungal partner.

The fungus usually gives a lichen its overall shape and structure, and tissues formed by hyphae account for most of the lichen's mass. The cells of the alga or cyanobacterium generally occupy an inner layer below the lichen surface **(Figure 31.25)**. The merger of fungus and alga or cyanobacterium is so complete that lichens are given scientific names as though they were single organisms. As might be expected of such "dual organisms," asexual reproduction as a symbiotic unit is common. This can occur either by fragmentation of the parental lichen or by the formation of **soredia** (singular, *soredium*), small clusters of hyphae with embedded algae (see Figure 31.25). The fungi of many lichens also reproduce sexually.

In most lichens, each partner provides something the other could not obtain on its own. The alga or cyanobacterium provides carbon compounds; a cyanobacterium also fixes nitrogen (see Concept 27.3) and provides organic



▶ Figure 31.25 Anatomy of an ascomycete lichen. (colorized SEM)

nitrogen compounds. The fungus provides its photosynthetic partner with a suitable environment for growth. The physical arrangement of hyphae allows for gas exchange, protects the photosynthetic partner, and retains water and minerals, most of which are absorbed from airborne dust or from rain. The fungus also secretes acids, which aid in the uptake of minerals.

Lichens are important pioneers on cleared rock and soil surfaces, such as volcanic flows and burned forests. They break down the surface by physically penetrating and chemically attacking it, and they trap windblown soil. Nitrogen-fixing lichens also add organic nitrogen to some ecosystems. These processes make it possible for a succession of plants to grow. Fossils show that lichens were on land 420 million years ago. These early lichens may have modified rocks and soil much as they do today, helping pave the way for plants.

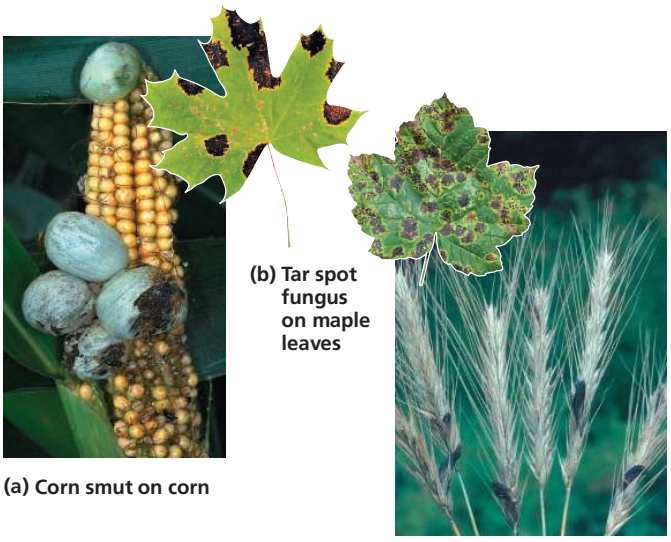
Fungi as Parasites

Like mutualistic fungi, parasitic fungi absorb nutrients from the cells of living hosts, but they provide no benefits in return. About 30% of the 145,000 known species of fungi make a living as parasites or pathogens, mostly of plants **(Figure 31.26)**. An example of a plant pathogen is *Cryphonectria parasitica*, the ascomycete fungus that causes chestnut blight, which dramatically changed the landscape of the northeastern United States. Accidentally introduced via trees imported from Asia in the early 1900s, spores of the fungus entered cracks in the bark of American chestnut trees and produced hyphae, killing many trees. The once-common chestnuts now survive mainly as sprouts from the stumps of former trees. Another ascomycete, *Fusarium circinatum*, causes pine pitch canker, a disease that threatens pines throughout the world. In addition, between 10% and 50% of the world's fruit harvest is lost annually due to fungi, and grain crops also suffer major losses each year.

Some fungi that attack food crops produce compounds that are toxic to humans. One example is the ascomycete *Claviceps purpurea*, which grows on rye plants, forming purple structures called ergots (see Figure 31.26c). If infected rye is milled into flour, toxins from the ergots can cause ergotism, characterized by gangrene, nervous spasms, burning sensations, hallucinations, and temporary insanity. An epidemic of ergotism around 944 CE killed up to 40,000 people in France. One compound that has been isolated from ergots is lysergic acid, the raw material from which the hallucinogen LSD is made.

Although animals are less susceptible to parasitic fungi than are plants, about 1,000 fungi are known to parasitize animals. Two such parasites, the chytrids *Batrachochytrium dendrobatidis* (discovered in 1998) and *B. salamandrivorans* (discovered in 2013; this species primarily attacks salamanders), have been implicated in the recent decline or extinction of 500 species of frogs and other amphibians. These chytrids can cause severe skin infections, leading

▼ Figure 31.26 Examples of fungal diseases of plants.

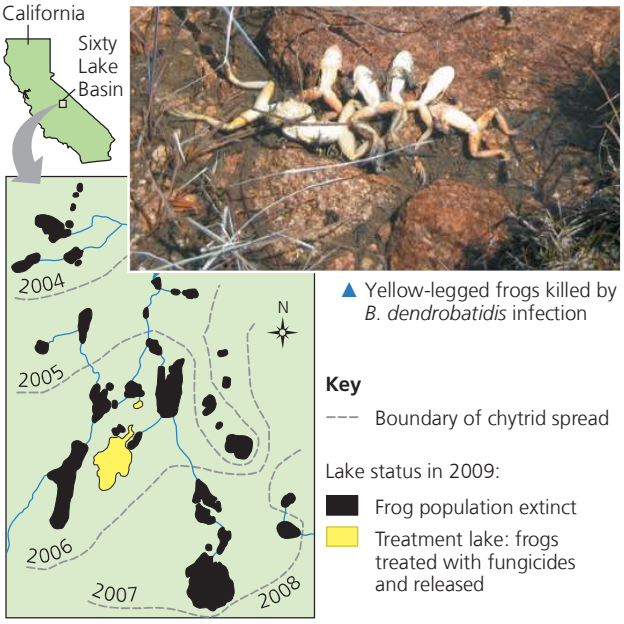


(a) Corn smut on corn

(b) Tar spot fungus on maple leaves

(c) Ergots on rye

▼ Figure 31.27 Amphibians under attack. The number of yellow-legged frogs (*Rana muscosa*) plummeted after the chytrid *Batrachochytrium dendrobatidis* reached the Sixty Lake Basin area of California. In the years leading up to the chytrid's 2004 arrival, there had been more than 2,300 frogs in these lakes. By 2009, only 38 frogs remained; all the survivors were in two lakes (yellow) where frogs had been treated with a fungicide to reduce the chytrid's impact.



▲ Yellow-legged frogs killed by *B. dendrobatidis* infection

INTERPRET THE DATA *Do the data depicted indicate that the chytrid caused or is correlated to the drop in frog numbers? Explain.*

to massive die-offs **(Figure 31.27)**. Field observations and studies of museum specimens show that *B. dendrobatidis* and *B. salamandrivorans* first appeared in amphibian populations shortly before their declines in Australia, Costa Rica, Germany, the United States, and other countries. Genetic analyses indicate that both *B. dendrobatidis* and *B. salamandrivorans* originated in Asia and spread from there via the commercial trade of frogs and salamanders.

The general term for an infection in an animal by a fungal parasite is **mycosis**. In humans, skin mycoses include the disease ringworm, so named because it appears as circular red areas on the skin. Most commonly, the ascomycetes that cause ringworm grow on the feet, causing the intense itching and blisters known as athlete's foot. Though highly contagious, athlete's foot and other ringworm infections can be treated with fungicidal lotions and powders.

Systemic mycoses, by contrast, spread through the body and usually cause very serious illnesses. They are typically caused by inhaled spores. For example, coccidioidomycosis is a systemic mycosis that produces tuberculosis-like symptoms in the lungs. Each year, hundreds of cases in North America require treatment with antifungal drugs, without which the disease could be fatal.

Some mycoses are opportunistic, occurring only when a change in the body's microorganisms, chemical environment, or immune system allows fungi to grow unchecked. *Candida albicans*, for example, is one of the normal inhabitants of moist epithelia, such as the vaginal lining. Under certain circumstances, *C. albicans* can grow too rapidly and become pathogenic, leading to so-called "yeast infections." A related species, *C. auris*, has emerged as a global threat, often in healthcare facilities. Resistant to multiple antifungal drugs, this species can infect the bloodstream and cause life-threatening infections.

Practical Uses of Fungi

The dangers posed by fungi should not overshadow their immense benefits. We depend on their ecological services as decomposers and recyclers of organic matter. In addition, mushrooms are not the only fungi of interest for human consumption. Fungi are used to ripen Roquefort and other blue cheeses. Morels and truffles, the edible fruiting bodies of various ascomycetes, are highly prized for their complex flavors (see Figure 31.17). These fungi can sell for hundreds to thousands of dollars a pound. Truffles release strong odors that attract mammals and insects, which in nature feed on them and disperse their spores. In some cases, the odors mimic the pheromones (sex attractants) of certain mammals. For example, the odors of several European truffles mimic the pheromones released by male pigs, which explains why truffle hunters sometimes use female pigs to help find these delicacies.

Humans have used yeasts to produce alcoholic beverages and bread for thousands of years. Under anaerobic conditions, yeasts ferment sugars to alcohol and CO_2, which causes dough to rise. Only relatively recently have the yeasts involved been separated into pure cultures for more controlled use. The yeast *Saccharomyces cerevisiae* is the most important of all cultured fungi (see Figure 31.7). It is available as many strains of baker's yeast and brewer's yeast.

Many fungi have great medical value as well. For example, a compound extracted from ergots is used to reduce high blood pressure and to stop maternal bleeding after childbirth. Some fungi produce antibiotics that are effective in treating bacterial infections. In fact, the first antibiotic discovered was penicillin, made by the ascomycete mold *Penicillium*. Other examples of pharmaceuticals derived from fungi include cholesterol-lowering drugs and cyclosporine, a drug used to suppress the immune system after organ transplants.

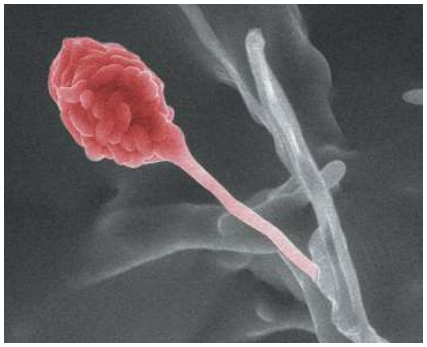
Fungi also figure prominently in basic research. For example, the yeast *Saccharomyces cerevisiae* is used to study the

molecular genetics of eukaryotes because its cells are easy to culture and manipulate. Scientists are gaining insight into the genes involved in Parkinson's disease by examining the functions of homologous genes in *S. cerevisiae*.

Genetically modified fungi also hold much promise. For example, scientists have succeeded in engineering a strain of *S. cerevisiae* that produces human glycoproteins, including insulin-like growth factor. Such fungus-produced glycoproteins have the potential to treat people with medical conditions that prevent them from producing these compounds. Meanwhile, other researchers are sequencing the genome of *Gliocladium roseum*, an ascomycete that can grow on wood or agricultural waste and that naturally produces hydrocarbons similar to those in diesel fuel **(Figure 31.28)**. They hope to decipher the metabolic pathways by which *G. roseum* synthesizes hydrocarbons, with the goal of harnessing those pathways to produce biofuels without reducing land area for growing food crops (as occurs when ethanol is produced from corn).

Having now completed our survey of the kingdom Fungi, we will turn in the rest of this unit to the closely related kingdom Animalia, to which we humans belong.

▶ Figure 31.28 Can this fungus be used to produce biofuels? The ascomycete *Gliocladium roseum* can produce hydrocarbons similar to those in diesel fuel (colorized SEM).



CONCEPT CHECK 31.5

1. What are some of the benefits that lichen algae can derive from their relationship with fungi?
2. What characteristics of pathogenic fungi result in their being efficiently transmitted?
3. **WHAT IF?** How might life on Earth differ from what we know today if no mutualistic relationships between fungi and other organisms had ever evolved?

For suggested answers, see Appendix A.

31 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

CONCEPT 31.1

Fungi are heterotrophs that feed by absorption *(pp. 655–657)*

- All **fungi** (including decomposers and symbionts) are heterotrophs that acquire nutrients by absorption. Many fungi secrete enzymes that break down complex molecules.
- Most fungi grow as thin, multicellular filaments called **hyphae**; relatively few species grow only as single-celled **yeasts**. In their multicellular form, fungi consist of **mycelia**, networks of branched hyphae adapted for absorption. Mycorrhizal fungi have specialized hyphae that enable them to form a mutually beneficial relationship with plants.

? *How does the morphology of multicellular fungi affect the efficiency of nutrient absorption?*

CONCEPT 31.2

Fungi produce spores through sexual or asexual life cycles *(pp. 657–659)*

- In fungi, the sexual life cycle involves cytoplasmic fusion (**plasmogamy**) and nuclear fusion (**karyogamy**), with an intervening **heterokaryotic** stage in which cells have haploid nuclei from two parents. The diploid cells resulting from karyogamy are short-lived and undergo meiosis, producing genetically diverse haploid **spores**.
- Many fungi can reproduce asexually as filamentous fungi or yeasts.

DRAW IT *Draw a generalized fungal life cycle, labeling asexual and sexual reproduction, meiosis, plasmogamy, karyogamy, and the points in the cycle when spores and the zygote are produced.*

CONCEPT 31.3

The ancestor of fungi was an aquatic, single-celled, flagellated protist *(pp. 659–660)*

- Molecular evidence indicates that fungi and animals diverged over a billion years ago from a common unicellular ancestor that had a flagellum. However, the oldest fossils that are widely accepted as fungi are 440 million years old.
- Chytrids and other basal fungal lineages have flagellated spores.
- Fungi were among the earliest colonizers of land; fossil evidence indicates that these colonizers included species that were symbionts with early plants.

? *Did multicellularity originate independently in fungi and animals? Explain.*

CONCEPT 31.4

Fungi have radiated into a diverse set of lineages

(pp. 660–667)

Fungal Phylum	Distinguishing Features
Cryptomycota (**cryptomycetes**)	Parasites with flagellated spores 
Microsporidia (**microsporidians**)	Parasitic cells that form resistant spores 
Chytridiomycota (**chytrids**)	Flagellated spores 
Zoopagomycota (**zoopagomycetes**)	Resistant zygosporangium as sexual stage 
Mucuromycota (**mucuromycetes**)	Include fungi that form arbuscular mycorrhizae with plants 
Ascomycota (**ascomycetes**)	Sexual spores (ascospores) borne internally in sacs called asci; vast numbers of asexual spores (conidia) produced 
Basidiomycota (**basidiomycetes**)	Elaborate fruiting body (basidiocarp) containing many basidia that produce sexual spores (basidiospores) 

DRAW IT *Draw a phylogenetic tree of the major groups of fungi.*

CONCEPT 31.5

Fungi play key roles in nutrient cycling, ecological interactions, and human welfare *(pp. 667–671)*

- Fungi perform essential recycling of chemical elements between the living and nonliving world.
- **Lichens** are highly integrated symbiotic associations of fungi and algae or cyanobacteria.
- Many fungi are parasites, mostly of plants.
- Humans use fungi for food and to make antibiotics.

? *How are fungi important as decomposers, mutualists, and pathogens?*

TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

1. *All* fungi are
   (A) symbiotic. (C) flagellated.
   (B) heterotrophic. (D) decomposers.
2. Which of the following cells or structures are associated with *asexual* reproduction in fungi?
   (A) ascospores (C) zygosporangia
   (B) basidiospores (D) conidiophores
3. The closest relatives of fungi are thought to be the
   (A) animals. (C) mosses.
   (B) vascular plants. (D) slime molds.

Levels 3-4: Applying/Analyzing

4. The most important adaptive advantage associated with the filamentous nature of fungal mycelia is
   (A) the ability to form haustoria and parasitize other organisms.
   (B) the potential to inhabit almost all terrestrial habitats.
   (C) the increased chance of contact between mating types.
   (D) an extensive surface area well suited for invasive growth and absorptive nutrition.
5. **SCIENTIFIC INQUIRY • INTERPRET THE DATA** The grass *Dichanthelium lanuginosum* lives in hot soils and houses fungi of the genus *Curvularia* as endophytes. Researchers tested the impact of *Curvularia* on the heat tolerance of this grass. They grew plants without (E–) and with (E+) *Curvularia* endophytes at different temperatures and measured plant mass and the number of new shoots the plants produced. Draw a bar graph for plant mass versus temperature and interpret it.

Soil Temp.	*Curvularia* + or –	Plant Mass (g)	No. of New Shoots
30°C	E–	16.2	32
	E+	22.8	60
35°C	E–	21.7	43
	E+	28.4	60
40°C	E–	8.8	10
	E+	22.2	37
45°C	E–	0	0
	E+	15.1	24

Data from R. S. Redman et al., Thermotolerance generated by plant/fungal symbiosis, *Science* 298:1581 (2002).

Levels 5-6: Evaluating/Creating

6. **EVOLUTION CONNECTION** The fungus-alga symbiosis that makes up a lichen is thought to have evolved multiple times independently in different fungal groups. However, lichens fall into three well-defined growth forms (see Figure 31.24). How could you test the following hypotheses? Hypothesis 1: Crustose, foliose, and fruticose lichens each represent a monophyletic group. Hypothesis 2: Each lichen growth form represents convergent evolution by diverse fungal groups.
7. **WRITE ABOUT A THEME: ORGANIZATION** As you read in this chapter, fungi have long formed symbiotic associations with plants and with algae. In a short essay (100–150 words), describe how these two types of associations may lead to emergent properties in biological communities.
8. **SYNTHESIZE YOUR KNOWLEDGE**



This wasp is the unfortunate victim of an entomopathogenic fungus (a parasitic fungus of insects). Write a paragraph describing what this image illustrates about the nutritional mode, body structure, and ecological role of the fungus.

For selected answers, see Appendix A.

32 An Overview of Animal Diversity

KEY CONCEPTS

32.1 **Animals are multicellular, heterotrophic eukaryotes with tissues that develop from embryonic layers** *p. 674*

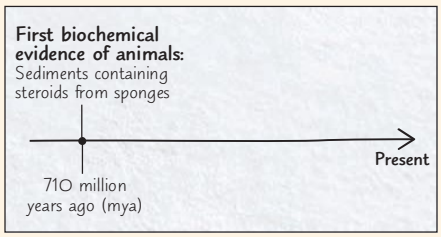
32.2 **The history of animals spans more than half a billion years** *p. 675*

32.3 **Animals can be characterized by body plans** *p. 679*

32.4 **Views of animal phylogeny continue to be shaped by new molecular and morphological data** *p. 682*

Study Tip

Draw a time line: Create a time line like the one shown here, and mark when the following occurred: first biochemical evidence of animals, Edicaran biota, Cambrian explosion, colonization of land by vertebrates, and dinosaur extinction. Briefly describe the significance of each event.



Go to Mastering Biology

For Students (in eText and Study Area)
- Get Ready for Chapter 32
- Interview with Nicole King: Investigating the ancestry of choanoflagellates

For Instructors to Assign (in Item Library)
- Tutorial: Visualizing Animal Body Symmetry and Axes
- Tutorial: Animal Body Plans
- Scientific Skills Exercise: Calculating and Interpreting Correlation Coefficients

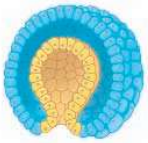


Figure 32.1 This chameleon can wield its long, sticky tongue with blinding speed to capture its prey. Other predatory animals use strength, concealed traps, or toxins to capture prey. Likewise, herbivorous animals can strip plants bare of leaves or seeds, while parasitic animals weaken their hosts by consuming their tissues or body fluids. Overall, we can think of animals as a kingdom of consumers.

What key characteristics of animals make them such efficient consumers?

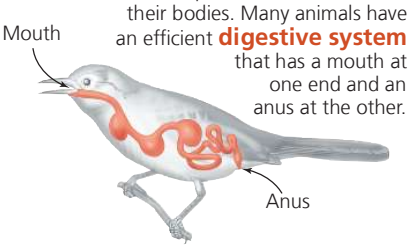


Animals are **heterotrophs**: They obtain energy and nutrients by eating other organisms.

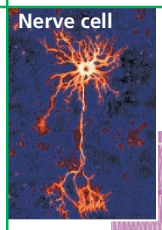


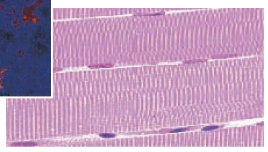
Animal embryo (cross section)

Animals have **tissues**, collections of specialized cells that function as a unit. Tissues form from layers of embryonic cells.



Animals process their food inside their bodies. Many animals have an efficient **digestive system** that has a mouth at one end and an anus at the other.





Muscle cells

The tissues of animals include those composed of unique **nerve and muscle cells**.



Their nerve and muscle cells enable animals to **move** as well as to **detect and capture** potential prey.

CONCEPT 32.1

Animals are multicellular, heterotrophic eukaryotes with tissues that develop from embryonic layers

Listing features shared by all animals is challenging, as there are exceptions to nearly every criterion we might select. When taken together, however, several characteristics of animals sufficiently describe the group for our discussion.

Nutritional Mode

Animals differ from both plants and fungi in their mode of nutrition. Plants are autotrophic eukaryotes capable of generating organic molecules through photosynthesis. Fungi are heterotrophs that grow on or near their food and that feed by absorption (often after they have released enzymes that digest the food outside their bodies). Unlike plants, animals cannot construct all of their own organic molecules, and so, in most cases, they ingest them—either by eating other living organisms or by eating nonliving organic material. But unlike fungi, most animals feed by ingesting their food and then using enzymes to digest it within their bodies.

Cell Structure and Specialization

Animals are eukaryotes, and like plants and most fungi, animals are multicellular. In contrast to plants and fungi, however, animals lack the structural support of cell walls. Instead, proteins external to the cell membrane provide structural support to animal cells and connect them to one another (see Figure 6.28). The most abundant of these proteins is collagen, which is not found in plants or fungi.

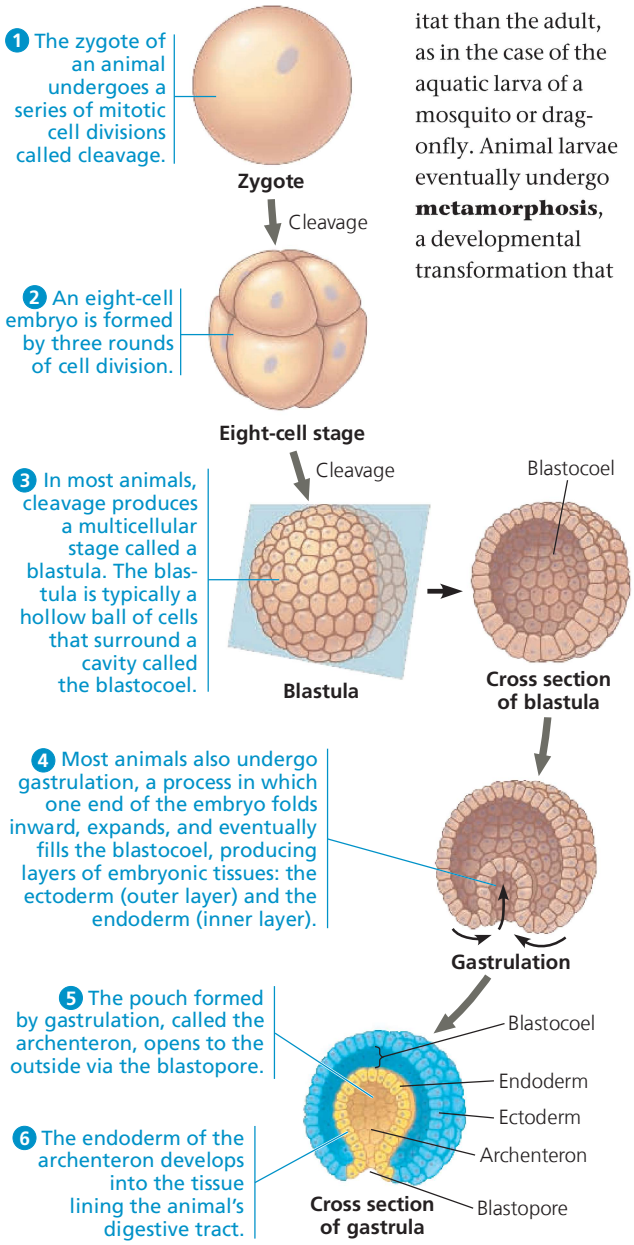
The cells of most animals are organized into **tissues**, groups of similar cells that act as a functional unit. For example, muscle tissue and nervous tissue are responsible for moving the body and conducting nerve impulses, respectively. The ability to move and conduct nerve impulses underlies many of the adaptations that differentiate animals from plants and fungi (which lack muscle and nerve cells). For this reason, muscle and nerve cells are central to the animal lifestyle.

Reproduction and Development

Most animals reproduce sexually, and the diploid stage usually dominates the life cycle. In the haploid stage, sperm and egg cells are produced directly by meiotic division, unlike what occurs in plants and fungi (see Figure 13.6). In most animal species, a small, flagellated sperm fertilizes a larger, nonmotile egg, forming a diploid zygote. The zygote then undergoes **cleavage**, a succession of mitotic cell divisions without cell growth between the divisions. During the development of most animals, cleavage leads to the formation of a multicellular embryonic stage called a **blastula**, which in many animals takes the form of a hollow ball **(Figure 32.2)**. Following this stage is the process of **gastrulation**, during which the layers of embryonic tissues that will develop into adult body parts are produced (see also Figure 47.8). The resulting developmental stage is called a **gastrula**.

Although some animals, including humans, develop directly into adults, the life cycles of most animals include at least one larval stage. A **larva** is a sexually immature form of an animal that is morphologically distinct from the adult, usually eats different food, and may even have a different habitat than the adult, as in the case of the aquatic larva of a mosquito or dragonfly. Animal larvae eventually undergo **metamorphosis**, a developmental transformation that

▼ Figure 32.2 Early embryonic development in animals.



turns the animal into a juvenile that resembles an adult but is not yet sexually mature.

Though adult animals vary widely in morphology, the genes that control animal development are similar across a broad range of taxa. All animals have developmental genes that regulate the expression of other genes, and many of these regulatory genes contain sets of DNA sequences called *homeoboxes* (see Concept 21.6). In particular, most animals share a unique homeobox-containing family of genes, known as *Hox* genes. *Hox* genes play important roles in the development of animal embryos, controlling the expression of many other genes that influence morphology.

CONCEPT CHECK 32.1

1. Summarize the main stages of animal development. What family of control genes plays a major role?
2. **WHAT IF?** What animal characteristics would be needed by an imaginary plant that could chase, capture, and digest its prey—yet could also extract nutrients from soil and conduct photosynthesis?

For suggested answers, see Appendix A.

CONCEPT 32.2

The history of animals spans more than half a billion years

To date, biologists have identified 1.3 million extant species of animals, and estimates of the actual number run far higher. This vast diversity encompasses a spectacular range of morphological variation, from corals to cockroaches to crocodiles. Various studies suggest that this great diversity originated during the last billion years. For example, researchers have unearthed 710-million-year-old sediments containing chemical evidence of steroids that today are primarily produced by a particular group of sponges. Since sponges are animals, these "fossil steroids" suggest that animals had arisen by 710 million years ago.

DNA analyses generally agree with this fossil biochemical evidence; for example, one recent molecular clock study estimated that sponges originated about 700 million years ago. These findings are also consistent with molecular analyses suggesting that the common ancestor of all extant animal species lived about 770 million years ago. What was this common ancestor like, and how did animals arise from their single-celled ancestors?

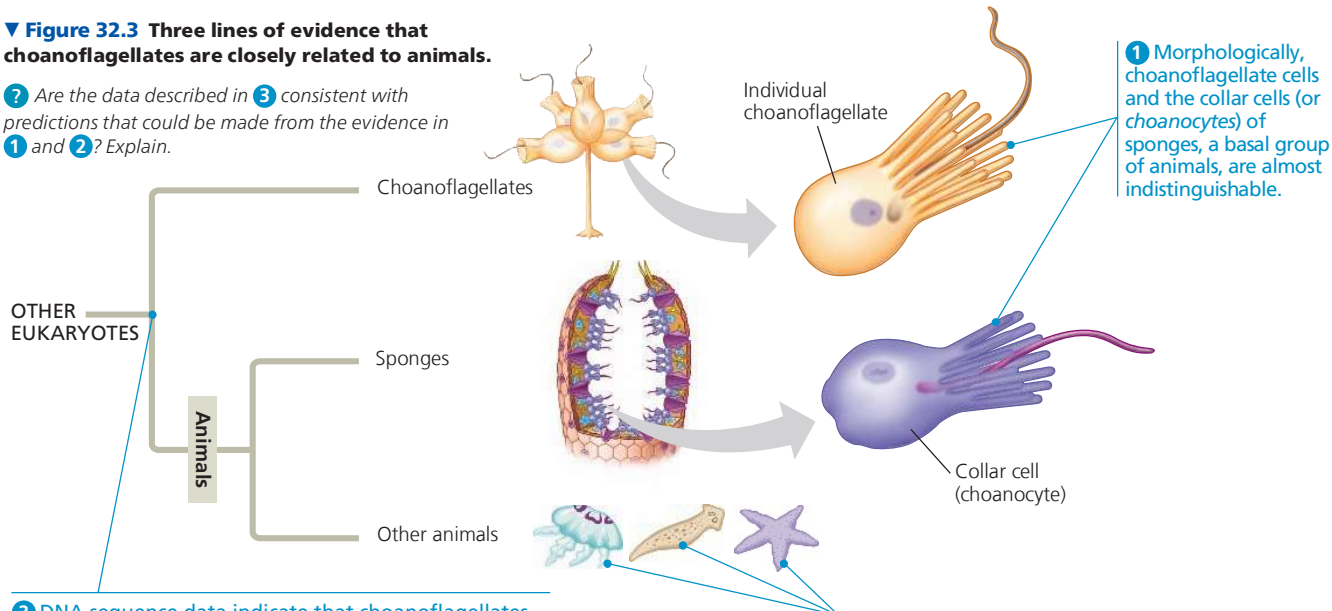
Steps in the Origin of Multicellular Animals

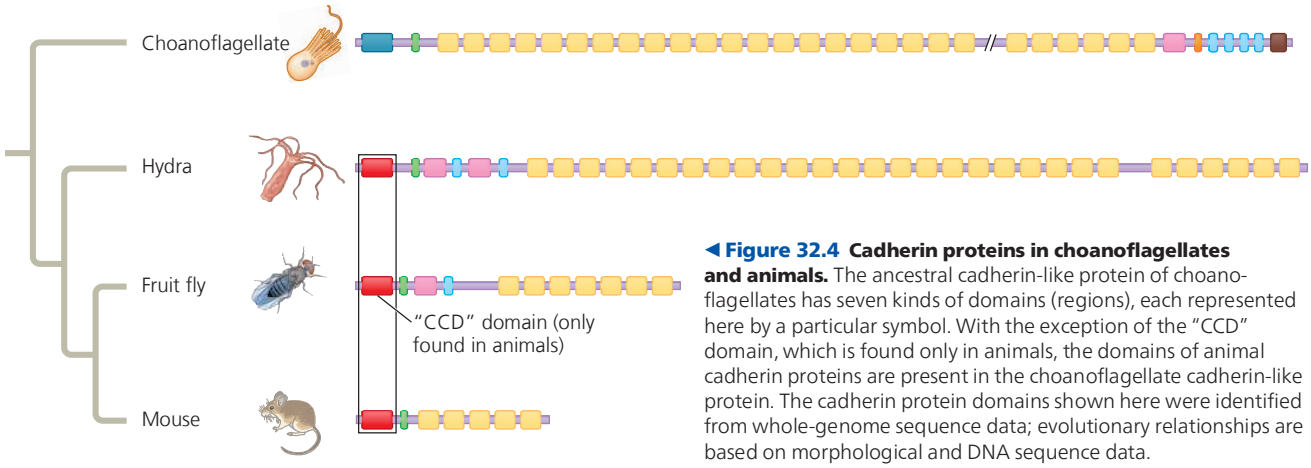
One way to gather information about the origin of animals is to identify protist groups that are closely related to animals. As shown in **Figure 32.3**, morphological and molecular evidence point to choanoflagellates as the closest living relatives of animals. Based on such evidence, researchers have hypothesized that the common ancestor of choanoflagellates and living animals may have been a suspension feeder similar to present-day choanoflagellates.

Scientists exploring *how* animals may have arisen from their single-celled ancestors have noted that the origin of multicellularity requires the evolution of new ways for cells to adhere (attach) and signal (communicate) to each other. To learn more about such mechanisms, researchers compared

▼ Figure 32.3 Three lines of evidence that choanoflagellates are closely related to animals.

? Are the data described in 3 consistent with predictions that could be made from the evidence in 1 and 2? Explain.





◀ Figure 32.4 Cadherin proteins in choanoflagellates and animals. The ancestral cadherin-like protein of choanoflagellates has seven kinds of domains (regions), each represented here by a particular symbol. With the exception of the "CCD" domain, which is found only in animals, the domains of animal cadherin proteins are present in the choanoflagellate cadherin-like protein. The cadherin protein domains shown here were identified from whole-genome sequence data; evolutionary relationships are based on morphological and DNA sequence data.

the genome of the unicellular choanoflagellate *Monosiga brevicollis* with those of representative animals. This analysis uncovered 78 protein domains in *M. brevicollis* that were otherwise only known to occur in animals. (A *domain* is a key structural or functional region of a protein.) For example, *M. brevicollis* has genes that encode domains of certain proteins (known as cadherins) that play key roles in how animal cells attach to one another, as well as genes that encode protein domains that animals (and only animals) use in cell-signaling pathways.

Let's take a closer look at the cadherin attachment proteins we just mentioned. DNA sequence analyses show that animal cadherin proteins are composed primarily of domains that are also found in a cadherin-like protein of choanoflagellates **(Figure 32.4)**. However, animal cadherin proteins also contain a highly conserved region not found in the choanoflagellate protein (the "CCD" domain labeled in Figure 32.4). These data suggest that the cadherin attachment protein originated by the rearrangement of protein domains found in choanoflagellates plus the incorporation of a novel domain, the conserved CCD region. Overall, comparisons of choanoflagellate and animal genomes suggest that key steps in the transition to multicellularity in animals involved new ways of using proteins or parts of proteins that were encoded by genes found in choanoflagellates.

Next, we'll survey the fossil evidence for how animals evolved from their distant common ancestor over four geologic eras (see Table 25.1 to review the geologic time scale).

Mastering Biology
Interview with Nicole King: Investigating the ancestry of choanoflagellates



Neoproterozoic Era (1 Billion–541 Million Years Ago)

Although data from fossil steroids and molecular clocks indicate an earlier origin, the first generally accepted macroscopic fossils of animals date from about 560 million years ago. These fossils are members of an early group of mostly soft-bodied multicellular eukaryotes, known collectively as the **Ediacaran biota**. The name comes from the Ediacara Hills of Australia, where fossils of these organisms were first discovered **(Figure 32.5)**. Similar fossils have since been found on other continents. Among the oldest Ediacaran fossils that resemble animals, some have been classified as molluscs (snails and their relatives) or close relatives of the molluscs, while others are thought to be sponges or cnidarians (sea anemones and their relatives). Still others have proved difficult to classify, as they do not seem to be closely related to any living animal or algal groups. In addition to these macroscopic fossils, Neoproterozoic rocks have also yielded what may be microscopic fossils of early animal embryos. Although these microfossils appear to exhibit the basic structural organization of present-day animal



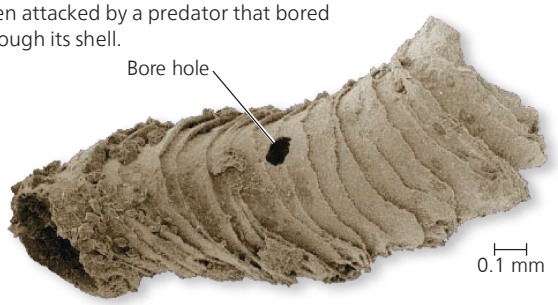
(a) *Dickinsonia costata* (animal phylum unknown)



(b) *Kimberella*, a mollusc (or close relative)

▲ Figure 32.5 Ediacaran fossil animals. Fossils dating to 560 million years ago document the earliest known macroscopic animals, including these two species.

▼ **Figure 32.6 Early evidence of predation.** This 550-million-year-old fossil of the animal *Cloudina* shows evidence of having been attacked by a predator that bored through its shell.



embryos, debate continues about whether these fossils are indeed of animals.

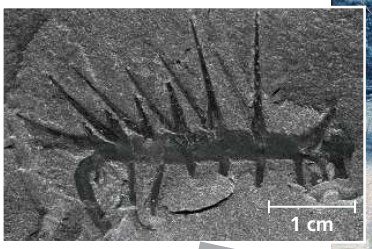
The fossil record from the Ediacaran period (635–541 million years ago) also provides early evidence of predation. Consider *Cloudina*, a small animal whose body was protected by a shell resembling a series of nested cones **(Figure 32.6)**. Some *Cloudina* fossils show signs of attack: round "bore holes" that resemble those formed today by predators that drill through the shells of their prey to gain access to the soft-bodied organisms lying within. Like *Cloudina*, some other small Ediacaran animals had shells or other defensive structures that may have been selected for by predators. Overall, the fossil evidence indicates that the Ediacaran was a time of increasing animal diversity—a trend that continued in the Paleozoic.

Paleozoic Era (541–252 Million Years Ago)

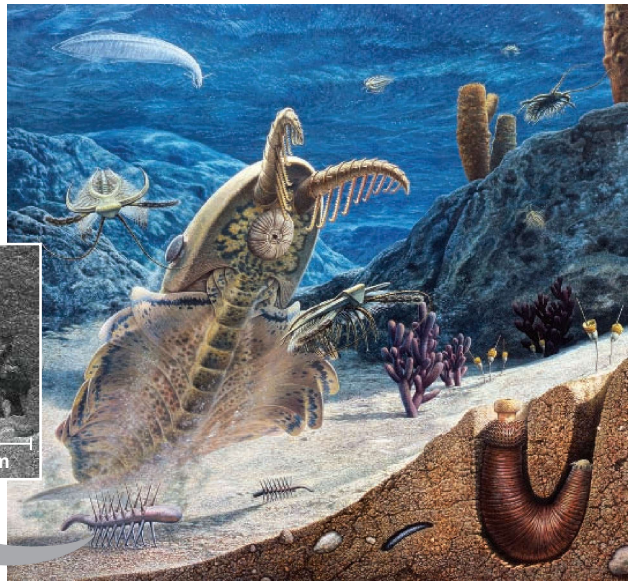
Another wave of animal diversification occurred 535–525 million years ago, early in the Cambrian period of the Paleozoic era—a phenomenon referred to as the **Cambrian explosion** (see Concept 25.3). In strata formed before the Cambrian explosion, only a few animal phyla have been observed. But in strata that are 535–525 million years old, paleontologists have found the oldest fossils of about half of all extant animal phyla, including the first arthropods, chordates, and echinoderms. Many of these fossils, which include the first large animals with hard, mineralized skeletons, look very different from most living animals **(Figure 32.7)**. Even so, paleontologists have established that these Cambrian fossils are members of extant animal phyla, or at least are close relatives. In particular, most of the fossils from the Cambrian explosion are of **bilaterians**, an enormous clade whose members (unlike sponges and cnidarians) typically have a two-sided or bilaterally symmetric form and a complete digestive tract, an efficient digestive system that has a mouth at one end and an anus at the other. As we'll discuss later in the chapter, bilaterians include molluscs, arthropods, chordates, and most other living animal phyla.

As the diversity of animal phyla increased during the Cambrian, the diversity of Ediacaran life-forms declined. What caused these trends? Fossil evidence suggests that during the early Cambrian period, as predators acquired novel adaptations for catching prey, such as claws, prey species acquired new defenses, such as protective shells. As new predator-prey relationships emerged, natural selection may have led to the decline of the soft-bodied Ediacaran species and the rise of various bilaterian phyla. Another hypothesis focuses on an increase in atmospheric oxygen that preceded the Cambrian explosion. More plentiful oxygen would have enabled animals with higher metabolic rates and larger body sizes to thrive, while potentially harming other species. A third hypothesis proposes that genetic changes affecting development, such as the origin of *Hox* genes and the addition of new microRNAs (small RNAs involved in gene regulation), facilitated the evolution of new body forms. In the **Scientific Skills Exercise**, you can investigate whether there is a correlation between microRNAs (miRNAs; see Figure 18.15) and body complexity in various animal phyla. These various hypotheses are not mutually exclusive; predator-prey relationships, atmospheric changes, and changes in development may each have played a role.

The Cambrian period was followed by the Ordovician, Silurian, and Devonian periods, when animal diversity continued to increase, although punctuated by episodes of mass extinction (see Figure 25.18). Vertebrates (fishes) emerged



508-million-year-old fossil of *Hallucigenia*



▲ **Figure 32.7 A Cambrian seascape.** This artist's reconstruction depicts a diverse array of organisms found in fossils from the Burgess Shale site in British Columbia, Canada. The animals include *Pikaia* (eel-like chordate at top left), *Marella* (small arthropod swimming at left), *Anomalocaris* (large animal with grasping limbs near a circular mouth), and *Hallucigenia* (animals with toothpick-like spikes on the seafloor and in inset).

Scientific Skills Exercise

Calculating and Interpreting Correlation Coefficients

Is Animal Complexity Correlated with miRNA Diversity? Animal phyla vary greatly in morphology, from simple sponges that lack tissues and symmetry to complex vertebrates. Members of different animal phyla have similar developmental genes, but the number of miRNAs varies considerably. In this exercise, you will explore whether miRNA diversity is correlated to morphological complexity.

How the Study Was Done In the analysis, miRNA diversity is represented by the average number of miRNAs in a phylum (x), while morphological complexity is represented by the average number of cell types (y). Researchers examined the relationship between these two variables by calculating the correlation coefficient (r). The correlation coefficient indicates the extent and direction of a linear relationship between two variables (x and y) and ranges in value between −1 and 1. When $r < 0$, x and y are negatively correlated, meaning that in a plot of the data points, values of y become smaller as values of x become larger. When $r > 0$, x and y are positively correlated (y becomes larger as x becomes larger). When $r = 0$, the variables are not correlated.

The formula for the correlation coefficient r is the following:

$$r = \frac{\sum (x_i - \bar{x})(y_i - \bar{y})}{(n - 1)(s_x s_y)}$$

In this formula, n is the number of observations, x_i is the value of the i^{th} observation of variable x, and y_i is the value of the i^{th} observation of variable y. $\bar{x}$ and $\bar{y}$ are the means of variables x and y, and s_x and s_y are the standard deviations of variables x and y. The $\sum$ symbol indicates that the n values of the product $(x_i - \bar{x})(y_i - \bar{y})$ are to be added together.

Data from the Study

Animal Phylum	i	No. of miRNAs (x_i)	$(x_i - \bar{x})$	$(x_i - \bar{x})^2$	No. of Cell Types (y_i)	$(y_i - \bar{y})$	$(y_i - \bar{y})^2$	$(x_i - \bar{x})(y_i - \bar{y})$
Porifera	1	5.8			25			
Platyhelminthes	2	35			30			
Cnidaria	3	2.5			34			
Nematoda	4	26			38			
Echinodermata	5	38.6			45			
Cephalochordata	6	33			68			
Arthropoda	7	59.1			73			
Urochordata	8	25			77			
Mollusca	9	50.8			83			
Annelida	10	58			94			
Vertebrata	11	147.5			172.5			
		$\bar{x}$ = s_x =		$\sum$ =	$\bar{y}$ = s_y =		$\sum$ =	$\sum$ =

Data from B. Deline et al., Evolution of metazoan morphological disparity, *Proceedings of the National Academy of Sciences USA* 115:E8909–E8918 (2018).

INTERPRET THE DATA

1. First, practice reading the data table. For the eighth observation ($i = 8$), what are x_i and y_i? For which phylum are these data?
2. Next, we'll calculate the mean and standard deviation for each variable (to review these topics, see the Scientific Skills Review in Appendix D). **(a)** The **mean** ($\bar{x}$) is the sum of the data values divided by n, the number of observations: $\bar{x} = \frac{\sum x_i}{n}$ Calculate the mean number of miRNAs ($\bar{x}$) and the mean number of cell types ($\bar{y}$) and enter them in the data table (to calculate $\bar{y}$, replace each x in the formula with a y). **(b)** Next, calculate $(x_i - \bar{x})$ and $(y_i - \bar{y})$ for each observation, recording your results in the appropriate column. Square each of those results to complete the $(x_i - \bar{x})^2$ and $(y_i - \bar{y})^2$ columns; sum the results for those columns. **(c)** Next, we'll calculate the **standard deviation**, s, which describes the variation found in a data set. Calculate s_x, the standard deviation of the miRNA data, using the following formula, where n = the number of observations. [Use the sum of $(x_i - \bar{x})^2$ you found in part (b).]

$$s_x = \sqrt{\frac{\sum (x_i - \bar{x})^2}{n - 1}}$$

   Repeat to find s_y by substituting y for x in this equation.
3. Next, we'll calculate the correlation coefficient r for the variables x and y. **(a)** First, use the results from question 2(b) to complete the $(x_i - \bar{x})(y_i - \bar{y})$ column; sum the results in that column. **(b)** Now find the product of $s_x s_y$ using your results from 2(c) above. Plug these values into the formula for r.
4. Do these data indicate that miRNA diversity and animal complexity are negatively correlated, positively correlated, or uncorrelated? Explain.
5. What does your analysis suggest about the role of miRNA diversity in the evolution of animal complexity?

Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

as the top predators of the marine food web. By 450 million years ago, groups that diversified during the Cambrian period began to make an impact on land. Arthropods were the first animals to adapt to terrestrial habitats, as indicated by fragments of arthropod remains and by well-preserved fossils from several continents of millipedes, centipedes, and spiders. Another clue is seen in fossilized fern galls—enlarged cavities that fern plants form in response to stimulation by resident insects, which then use the galls for protection. Fossils indicate that fern galls date back at least 302 million years, suggesting that insects and plants were influencing each other's evolution by that time.

Vertebrates colonized land around 365 million years ago and diversified into numerous terrestrial groups. Two of these survive today: the amphibians (such as frogs and salamanders) and the amniotes (reptiles, including birds, and

mammals). We will explore these groups, known collectively as the tetrapods, in more detail in Chapter 34.

Mesozoic Era (252–66 Million Years Ago)

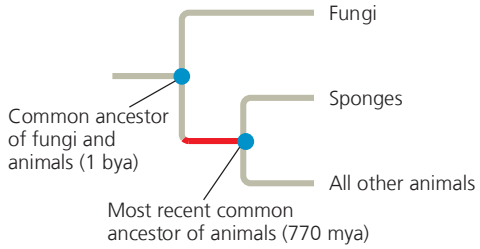
The animal phyla that had evolved during the Paleozoic began to spread into new habitats. In the oceans, the first coral reefs formed, providing other marine animals with new places to live. Some reptiles returned to the water, leaving plesiosaurs (see Figure 34.25) and other large aquatic predators as their descendants. On land, descent with modification in some tetrapods led to the origin of wings and other flight equipment in pterosaurs and birds. Large and small dinosaurs emerged, as both predators and herbivores. At the same time, the first mammals—tiny nocturnal insect-eaters—appeared on the scene. In addition, as you read in Concept 30.3, flowering plants (angiosperms) and insects both underwent dramatic diversifications during the late Mesozoic.

Cenozoic Era (66 Million Years Ago to the Present)

Mass extinctions of both terrestrial and marine animals ushered in a new era, the Cenozoic. Among the groups of species that disappeared were the large, nonflying dinosaurs and the marine reptiles. The fossil record of the early Cenozoic documents the rise of large mammalian herbivores and predators as mammals began to exploit the vacated ecological niches. The global climate gradually cooled throughout the Cenozoic, triggering significant shifts in many animal lineages. Among primates, for example, some species in Africa adapted to the open woodlands and savannas that replaced many of the former dense forests. The ancestors of our own species were among those grassland apes.

CONCEPT CHECK 32.2

1. Put the following milestones in animal evolution in order from oldest to most recent: (a) origin of mammals, (b) earliest evidence of terrestrial arthropods, (c) Ediacaran fauna, (d) extinction of large, nonflying dinosaurs.
2. **VISUAL SKILLS** Explain what is represented by the red-colored portion of the branch leading to animals. (See Figure 26.5, "Visualizing Phylogenetic Relationships," to review phylogenetic tree diagrams.)



3. **MAKE CONNECTIONS** Evaluate whether the origin of cell-to-cell attachment proteins in animals illustrates descent with modification. (See Concept 22.2.)

For suggested answers, see Appendix A.

CONCEPT 32.3

Animals can be characterized by body plans

Animal species vary tremendously in morphology, but their great diversity in form can be described by a relatively small number of major "body plans." A **body plan** is a particular set of morphological and developmental traits that are integrated into a functional whole—the living animal. The term *plan* here does not imply that animal forms are the result of conscious planning or invention. But body plans do provide a succinct way to compare and contrast key animal features. They also are of interest in the study of *evo-devo*, the interface between evolution and development.

Like all features of organisms, animal body plans have evolved over time. In some cases, including key stages in gastrulation, novel body plans emerged early in the history of animal life and have not changed since. As we'll discuss, however, other aspects of animal body plans have changed multiple times over the course of evolution. As we explore the major features of animal body plans, bear in mind that similar body forms may have evolved independently in different lineages. In addition, body features can be lost over the course of evolution, causing some closely related species to look very different from one another.

Symmetry

A basic feature of animal bodies is their type of symmetry—radial or bilateral—or absence of symmetry. (Many sponges, for example, lack symmetry altogether.) Use **Figure 32.8** to help you visualize radial and bilateral symmetry and how axes of orientation are used to describe the position of different parts of an animal's body.

The symmetry of an animal generally fits its lifestyle. Many radial animals are sessile (living attached to a substrate) or planktonic (drifting or weakly swimming, such as jellies, commonly called jellyfishes). Their symmetry equips them to meet the environment equally well from all sides. In contrast, bilateral animals typically move actively from place to place. Nearly all animals with a bilaterally symmetric body plan (such as arthropods and mammals) have sensory equipment concentrated at the head end of their body, including a central nervous system ("brain"). This central nervous system enables them to coordinate the complex movements involved in crawling, burrowing, flying, or swimming. Fossil evidence indicates that these two fundamentally different kinds of symmetry have existed for at least 550 million years.

Tissues

Animal body plans also vary with regard to tissue organization. Recall that tissues are collections of specialized cells that act as a functional unit. Sponges and a few other groups lack tissues. In all other animals, the embryo becomes layered during gastrulation (see Figure 47.8, "Visualizing Gastrulation,"

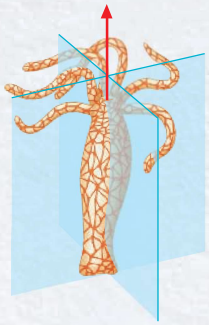
▼ Figure 32.8 VISUALIZING ANIMAL BODY SYMMETRY AND AXES

A basic feature of animal bodies is their type of symmetry. We'll focus on two common types of symmetry: radial symmetry and bilateral symmetry.

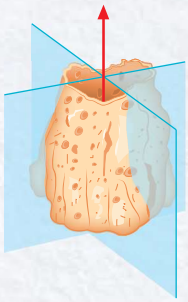
Radial Symmetry

The body parts of a radially symmetrical animal are arranged around a single main axis that passes through the center of the animal. Any imaginary slice through the central axis, as shown here in blue, divides the animal into mirror images.

1. ***Does a radial animal have a front side and a back side? A left side and a right side? Explain.***



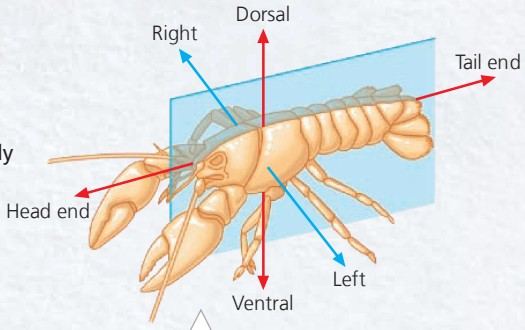
The symmetrical central body cavity of this hydra has a single opening (the "mouth/anus") surrounded by a circular rim of tentacles. Prey captured by the tentacles are pushed into the body cavity and digested.



Many sponges have an irregular shape, lacking symmetry altogether. But like this barrel sponge, some sponges exhibit radial symmetry, with their cells arranged in a regular pattern around a central axis.

Bilateral Symmetry and Body Axes

The body parts of a bilaterally symmetrical animal are arranged around two axes of orientation, the head-tail axis and the dorsal-ventral axis. Only one imaginary slice, again shown in blue, divides the animal into mirror-image halves, referred to as a right side and a left side.



Lobsters and other bilateral animals have a head end and a tail end, a dorsal (top) side and a ventral (bottom) side, as well as a right side and a left side. In nearly all bilateral animals, eyes and other sensory organs are concentrated in the head end of the body.



An upright posture evolved in some groups of bilateral animals, including humans and birds, such as the owl shown here.

2. ***Draw the two axes of orientation on this owl and label its head end, tail end, and dorsal, ventral, right, and left sides.***

Instructors: Additional questions related to this Visualizing Figure can be assigned in **Mastering Biology**.

which will help you understand this three-dimensional folding process). As development progresses, these layers, called *germ layers*, form the various tissues and organs of the body. **Ectoderm**, the germ layer covering the surface of the embryo, gives rise to the outer covering of the animal and, in some phyla, to the central nervous system. **Endoderm**, the innermost germ layer, lines the pouch that forms during gastrulation (the archenteron) and gives rise to the lining of the digestive tract (or cavity) and to the lining of organs such as the liver and lungs of vertebrates.

Cnidarians and a few other animal groups that have only these two germ layers are said to be **diploblastic**. All bilaterally symmetrical animals have a third germ layer, called the **mesoderm**, which fills much of the space between the ectoderm and endoderm. Thus, animals with bilateral symmetry are also said to be **triploblastic** (having three germ layers). In triploblasts, the mesoderm forms the muscles and most other organs between the digestive tract and the outer covering of the animal. Triploblasts include a broad range of animals, from flatworms to arthropods to vertebrates. (Although some diploblasts actually do have a third germ layer, it is not nearly as well developed as the mesoderm of animals considered to be triploblastic.)

Body Cavities

Nearly all animals have a **body cavity**, a fluid- or air-filled space located between the digestive tract (endoderm) and the outer body wall (ectoderm). Body cavities have diverse functions, such as to provide structural support and to facilitate the internal transport of nutrients, gases, and wastes.

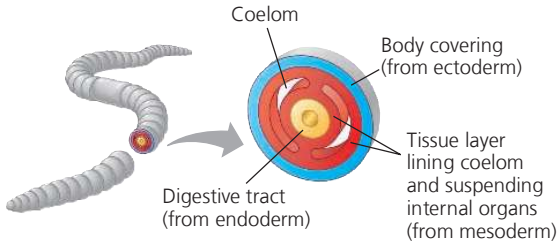
Many triploblastic animals have a **coelom** (from the Greek *koilos*, hollow), a body cavity that forms from tissue derived from mesoderm. The inner and outer layers of mesoderm that surround the cavity connect and form structures that suspend

the internal organs **(Figure 32.9a)**. A coelom's fluid cushions the suspended organs, helping to prevent internal injury. In soft-bodied animals, such as earthworms, the fluid in the coelom acts like a skeleton against which muscles can work. A coelom also enables the internal organs to grow and move independently of the outer body wall. If it were not for your coelom, for example, every beat of your heart or ripple of your intestine would warp your body's surface. Animals possessing coeloms are sometimes called *coelomates*.

Other triploblastic animals have a **hemocoel**, a body cavity that forms between the mesoderm and endoderm **(Figure 32.9b)**. A hemocoel contains *hemolymph*, a fluid that functions in the internal transport of nutrients and waste.

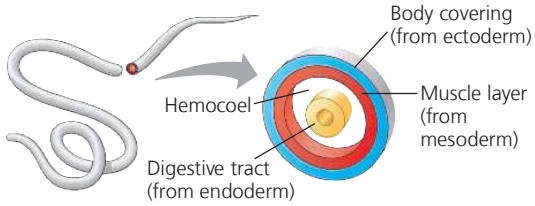
▼ Figure 32.9 Body cavities of triploblastic animals. The organ systems develop from the three embryonic germ layers.

(a) Coelom



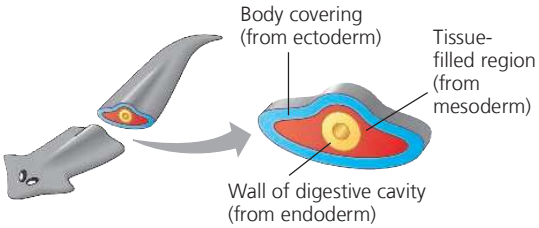
Many animals, including earthworms, have a coelom, a body cavity completely lined by tissue derived from mesoderm.

(b) Hemocoel



Roundworms and many other animals have a hemocoel, a body cavity lined by tissue derived from mesoderm and by tissue derived from endoderm.

(c) Compact (no body cavity)



Some animals, such as planarians, lack a body cavity between the digestive cavity and outer body wall.

Key

Ectoderm Mesoderm Endoderm

Hemolymph is analogous to your blood and is circulated through the body cavity in an open system by the heart.

Many animals have a hemocoel and a coelom. Molluscs, for instance, have a hemocoel as the primary body cavity, but they also have a reduced coelom that surrounds the heart and reproductive structures (see Figure 33.16). Other animals, such as rotifers and nematodes (see Figures 33.12 and 33.26), have only a hemocoel. Animals with only a hemocoel once were called *pseudocoelomates* (from the Greek *pseudo*, false) and the cavity, a pseudocoelom. Hemocoels and coeloms have been independently gained or lost multiple times in the course of animal evolution; hence, their presence or absence is not a good indicator of phylogenetic relationships.

Finally, some triploblastic animals lack a body cavity altogether **(Figure 32.9c)**. These compact animals tend to have thin, flat bodies. Such animals don't require an internal transport system: With bodies that are only a few cells thick, the exchange of nutrients, gases, and wastes can occur across the entire body surface. These animals are sometimes called *acoelomates* (from the Greek *a-*, without).

Protostome and Deuterostome Development

Many animals can be described as having one of two developmental modes: **protostome development** or **deuterostome development**. These modes can generally be distinguished by differences in cleavage, coelom formation, and fate of the blastopore.

Cleavage

Many animals with protostome development undergo **spiral cleavage**, in which the planes of cell division are diagonal to the vertical axis of the embryo; as seen in the eight-cell stage of the embryo, smaller cells are centered over the grooves between larger, underlying cells (**Figure 32.10a**, left). Furthermore, the so-called **determinate cleavage** of some animals with protostome development rigidly casts ("determines") the developmental fate of each embryonic cell very early. A cell isolated from a snail at the four-cell stage, for example, cannot develop into a whole animal. Instead, after repeated divisions, such a cell will form an inviable embryo that lacks many parts.

In contrast to the spiral cleavage pattern, deuterostome development is predominantly characterized by **radial cleavage**. The cleavage planes are either parallel or perpendicular to the vertical axis of the embryo; as seen at the eight-cell stage, the tiers of cells are aligned, one directly above the other (see Figure 32.10a, right). Most animals with deuterostome development also have **indeterminate cleavage**, meaning that each cell produced by early cleavage divisions retains the capacity to develop into a complete embryo. For example, if the cells of a sea urchin embryo are separated at the four-cell stage, each can form a complete larva. Similarly, it is the indeterminate cleavage of the human zygote that makes identical twins possible.

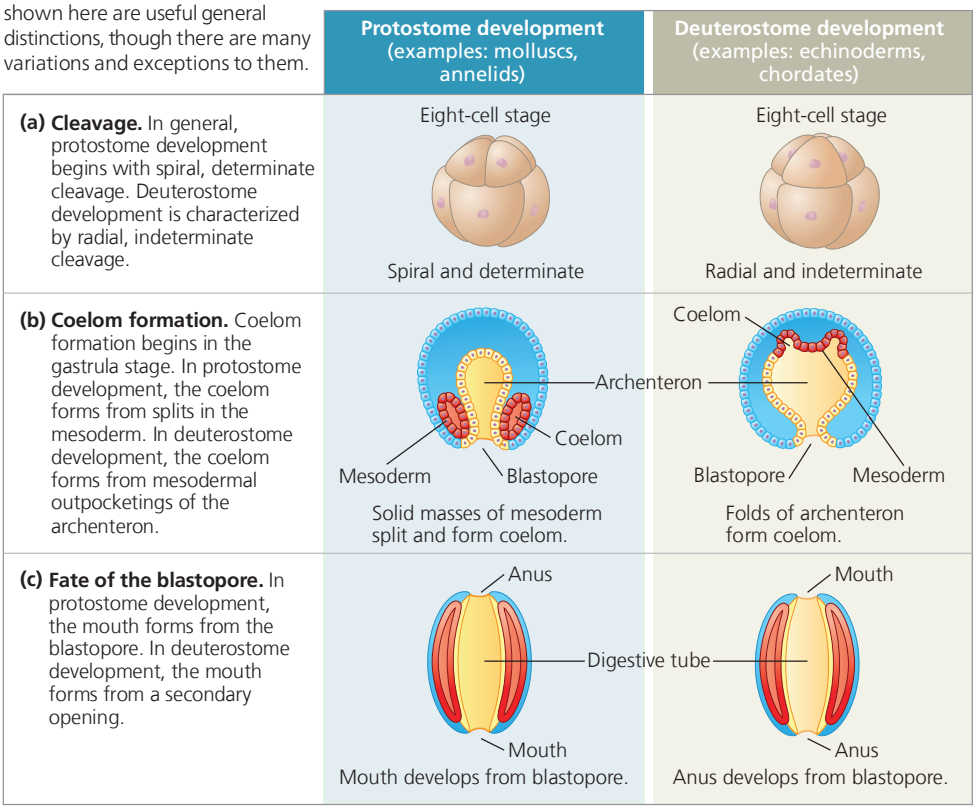
Coelom Formation

During gastrulation, an embryo's developing digestive tube initially forms as a blind pouch, the **archenteron**, which becomes the gut **(Figure 32.10b)**. As the archenteron forms in protostome development, initially solid masses of mesoderm split and form the coelom. In contrast, in deuterostome development, the mesoderm buds from the wall of the archenteron, and its cavity becomes the coelom.

Fate of the Blastopore

Protostome and deuterostome development often differ in the fate of the **blastopore**, the indentation that during gastrulation leads to the formation of the archenteron **(Figure 32.10c)**. After the archenteron develops, in most animals a second opening forms at the opposite end of the gastrula. In many species, the blastopore and this second opening become the two openings of the digestive tube: the mouth and the anus. In protostome development, the mouth generally develops from the first opening, the blastopore, and it is for this characteristic that the term *protostome* derives (from the Greek *protos*, first, and *stoma*, mouth). In deuterostome development (from the Greek *deuteros*, second), the mouth is derived from the secondary opening, and the blastopore usually forms the anus.

▼ Figure 32.10 Protostome and deuterostome development. The patterns shown here are useful general distinctions, though there are many variations and exceptions to them.



CONCEPT CHECK 32.3

1. Compare three aspects of the early development of a snail (a mollusc) and a human (a chordate).
2. Describe how animals that lack a body cavity exchange materials without an internal transport system.
3. **WHAT IF?** Evaluate this claim: Ignoring the details of their specific anatomy, worms, humans, and most other triploblasts have a shape analogous to that of a doughnut.

For suggested answers, see Appendix A.

CONCEPT 32.4

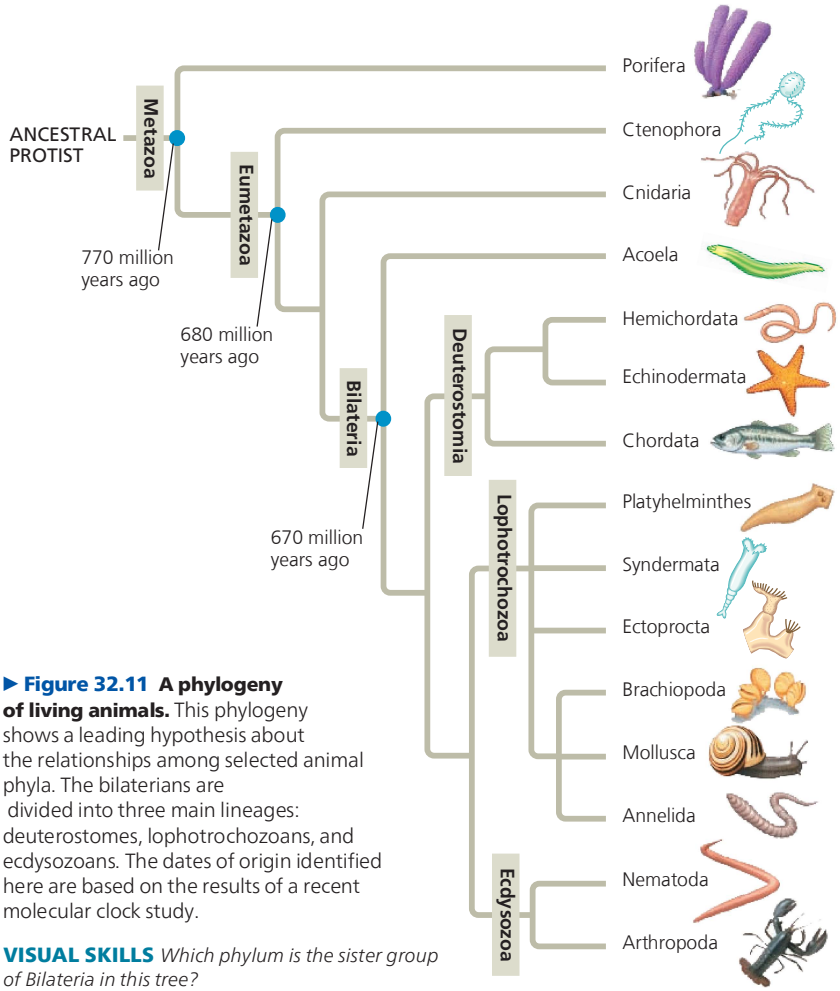
Views of animal phylogeny continue to be shaped by new molecular and morphological data

As animals with diverse body plans radiated during the early Cambrian, some lineages arose, thrived for a period of time, and then became extinct, leaving no descendants. However, by 500 million years ago, most animal phyla with members alive today were established. Next, we'll examine relationships among these taxa along with some remaining questions that are currently being addressed using genomic data.

The Diversification of Animals

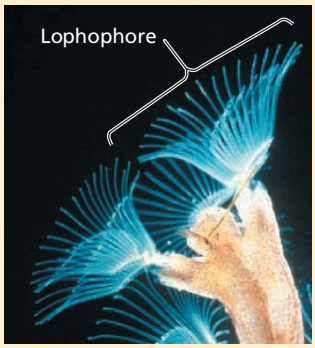
Zoologists currently recognize about three dozen phyla of extant animals, 15 of which are shown in **Figure 32.11**. Researchers infer evolutionary relationships among these phyla by analyzing whole genomes, as well as morphological traits, ribosomal RNA (rRNA) genes, *Hox* genes, protein-coding nuclear genes, and mitochondrial genes. Notice how the following points are reflected in Figure 32.11.

1. **All animals share a common ancestor.** Current evidence indicates that animals are monophyletic, forming a clade called Metazoa. All extant and extinct animal lineages have descended from a common ancestor.
2. **Sponges are the sister group to all other animals.** Sponges (phylum Porifera) are basal animals, having diverged from all other animals early in the history of the group. Recent morphological and phylogenomic analyses indicate that sponges are monophyletic, as shown here.

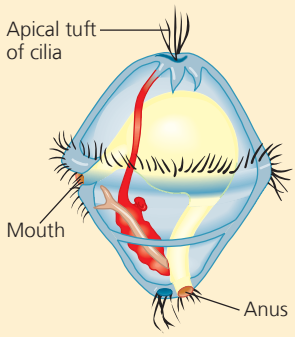


▶ Figure 32.11 A phylogeny of living animals. This phylogeny shows a leading hypothesis about the relationships among selected animal phyla. The bilaterians are divided into three main lineages: deuterostomes, lophotrochozoans, and ecdysozoans. The dates of origin identified here are based on the results of a recent molecular clock study.

VISUAL SKILLS *Which phylum is the sister group of Bilateria in this tree?*



(a) Lophophore feeding structures of an ectoproct



(b) Structure of a trochophore larva

▲ Figure 32.12 Morphological characteristics of lophotrochozoans.

3. **Eumetazoa is a clade of animals with tissues.** All animals except for sponges and a few others belong to a clade of **eumetazoans** ("true animals"). Members of this group have tissues, such as muscle tissue and nervous tissue. Basal eumetazoans, which include the phyla Ctenophora (comb jellies) and Cnidaria, are diploblastic and generally have radial symmetry.
4. **Most animal phyla belong to the clade Bilateria.** Bilateral symmetry and the presence of three prominent germ layers are shared derived characters that help define the clade Bilateria. This clade contains the majority of animal phyla, and its members are known as *bilaterians*. The Cambrian explosion was primarily a rapid diversification of bilaterians.
5. **There are three major clades of bilaterian animals.** Bilaterians have diversified into three main lineages, Deuterostomia, Lophotrochozoa, and Ecdysozoa. With one exception, the phyla in these clades consist entirely of **invertebrates**, animals that lack a backbone; Chordata is the only phylum that also includes **vertebrates**, animals with a backbone.

As depicted in Figure 32.11, hemichordates (acorn worms), echinoderms (sea stars and relatives), and chordates are members of the bilaterian clade **Deuterostomia**; thus, the term *deuterostome* refers not only to a mode of animal development, but also to the members of this clade. (The dual meaning of this term can be confusing since some organisms with a deuterostome developmental pattern are *not* members of clade Deuterostomia.) Hemichordates share some characteristics with chordates, such as gill slits and a dorsal nerve cord; echinoderms lack these characteristics. These shared traits may have been present in the common ancestor of the deuterostome clade (and lost in the echinoderm lineage). As mentioned above, phylum Chordata, the only phylum with vertebrate members, also includes invertebrates.

Bilaterians also diversified in two major clades that are composed entirely of invertebrates: the *lophotrochozoans* and the *ecdysozoans*. The name **Lophotrochozoa** refers to two different features observed in some animals belonging to this clade **(Figure 32.12)**. Some lophotrochozoans, such as ectoprocts, develop a unique structure called a **lophophore** (from the Greek *lophos*, crest, and *pherein*, to carry), a crown of

ciliated tentacles that function in feeding (see Figure 32.12a). Individuals in other phyla, including molluscs and annelids, go through a distinctive developmental stage called the **trochophore larva** (see Figure 32.12b)—hence the name lophotrochozoan.

The clade name **Ecdysozoa** refers to a characteristic shared by nematodes, arthropods, and some of the other ecdysozoan phyla that are not included in our survey. These animals secrete external skeletons (exoskeletons); the stiff covering of a cricket and the flexible cuticle of a nematode are examples. As the animal grows, it molts, squirming out of its old exoskeleton and secreting a larger one. The process of shedding the old exoskeleton is called *ecdysis*. Though named for this characteristic, the clade was proposed mainly on the basis of molecular data that support the common ancestry of its members. Furthermore, some taxa excluded from this clade by their molecular data, such as certain species of leeches, do in fact molt.

Future Directions in Animal Systematics

While many scientists think that current evidence supports the phylogeny in Figure 32.11, aspects continue to be debated. Although it can be frustrating that the phylogenies in textbooks are not set-in-stone truths, the uncertainty inherent in these diagrams is a healthy reminder that science is an ongoing, dynamic process of inquiry. We'll conclude with two questions that are the focus of ongoing research.

1. **Are ctenophores basal metazoans?** Many researchers have concluded that sponges are basal metazoans (see Figure 32.11). This conclusion was supported in a 2017 phylogenomic analysis, but several other studies have placed the comb jellies (phylum Ctenophora) at the base of the animal tree. In addition to the most recent phylogenomic results, data consistent with placing sponges at the base of the animal tree include fossil steroid evidence, molecular clock analyses, the morphological similarity of sponge collar cells to the cells of choanoflagellates (see Figure 32.3), and the fact that sponges are one of the few animal groups that lack tissues (as might be expected for basal animals). Ctenophores, on the other hand, have tissues, and their cells do not resemble the cells of choanoflagellates. At present, the idea that ctenophores are basal metazoans remains an intriguing but controversial hypothesis.
2. **Are the Acoela basal bilaterians?** A series of recent papers—including a 2016 phylogenomic study—have indicated that flatworms in phylum Acoela are basal bilaterians, as shown in Figure 32.11. A different conclusion was supported by one recent analysis, which placed members of the Acoela within Deuterostomia. Researchers are sequencing the genomes of additional species in the phylum and in closely related groups to provide a more definitive test of the hypothesis that the Acoela are basal bilaterians. If further evidence supports this hypothesis, bilaterians may have descended from a common ancestor that resembled this group of living flatworms—that is, an ancestor that had a simple nervous system, a saclike gut with a single opening (the "mouth"), and no excretory system.

CONCEPT CHECK 32.4

1. Describe the evidence that cnidarians share a more recent common ancestor with other animals than with sponges.
2. **WHAT IF?** Suppose ctenophores are basal metazoans and sponges are the sister group of all remaining animals. Under this hypothesis, redraw Figure 32.11 and discuss whether animals with tissues would form a clade.
3. **MAKE CONNECTIONS** Based on the phylogeny in Figure 32.11 and the information in Figure 25.11, evaluate this statement: "The Cambrian explosion actually consists of three explosions, not one."

For suggested answers, see Appendix A.

32 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

CONCEPT 32.1

Animals are multicellular, heterotrophic eukaryotes with tissues that develop from embryonic layers

(pp. 674–675)

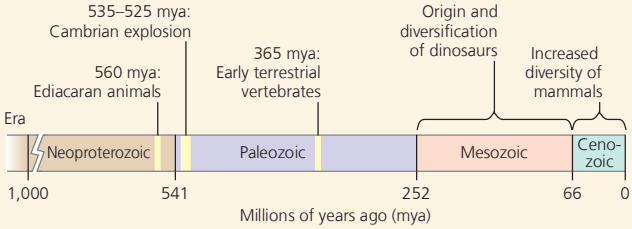
- Animals are heterotrophs that ingest their food.
- Animals are multicellular eukaryotes. Their cells are supported and connected to one another by collagen and other structural proteins located outside the cell membrane. Nervous tissue and muscle tissue are key animal features.
- In most animals, **gastrulation** follows the formation of the **blastula** and leads to the formation of embryonic tissue layers. Most animals have *Hox* genes that regulate the development of body form. Although *Hox* genes have been highly conserved over the course of evolution, they can produce a wide diversity of animal morphology.

? *Describe key ways that animals differ from plants and fungi.*

CONCEPT 32.2

The history of animals spans more than half a billion years *(pp. 675–679)*

- Fossil biochemical evidence and molecular clock analyses indicate that animals arose over 700 million years ago.
- Genomic analyses suggest that key steps in the origin of animals involved new ways of using proteins that were encoded by genes found in choanoflagellates.



? *What caused the Cambrian explosion? Describe current hypotheses.*

CONCEPT 32.3

Animals can be characterized by body plans *(pp. 679–682)*

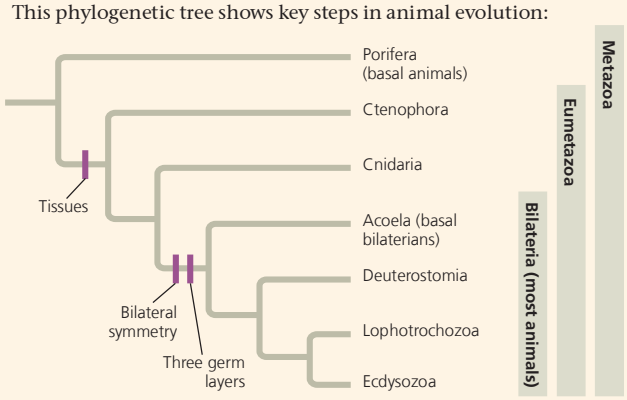
- Animals may lack symmetry or may have **radial** or **bilateral symmetry**. Bilaterally symmetrical animals have **dorsal** and **ventral** sides, as well as **head** and **tail** ends.
- Eumetazoan embryos may be **diploblastic** (two germ layers) or **triploblastic** (three germ layers). Triploblastic animals with a **body cavity** may have a **coelom** or a **hemocoel** (or both).
- **Protostome** and **deuterostome development** often differ in patterns of **cleavage**, coelom formation, and **blastopore** fate.

? *Describe how body plans provide useful information yet should be interpreted cautiously as evidence of evolutionary relationships.*

CONCEPT 32.4

Views of animal phylogeny continue to be shaped by new molecular and morphological data *(pp. 682–684)*

- This phylogenetic tree shows key steps in animal evolution:



? *Consider clades Bilateria, Lophotrochozoa, Metazoa, Chordata, Ecdysozoa, Eumetazoa, and Deuterostomia. List the clades to which humans belong in order from the most to the least inclusive clade.*

TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

1. One of the characteristics unique to animals is
   (A) gastrulation.
   (B) multicellularity.
   (C) sexual reproduction.
   (D) flagellated sperm.
2. The distinction between sponges and other animal phyla is based mainly on the absence versus the presence of
   (A) a body cavity.
   (B) a complete digestive tract.
   (C) mesoderm.
   (D) tissues.
3. Which of the following was probably an important factor in bringing about the Cambrian explosion?
   (A) the movement of animals onto land
   (B) an increase in the concentration of atmospheric nitrogen
   (C) the emergence of predator-prey relationships
   (D) the origin of bilaterian animals

Levels 3-4: Applying/Analyzing

4. Based on the tree in Figure 32.11, which statement is true?
   (A) The animal kingdom is not monophyletic.
   (B) The Acoela are more closely related to echinoderms than to annelids.
   (C) Sponges are basal animals.
   (D) Bilaterians do not form a clade.

Levels 5-6: Evaluating/Creating

5. **EVOLUTION CONNECTION** A professor begins a lecture on animal phylogeny (as shown in Figure 32.11) by saying, "We are all worms." In this context, what did she mean?
6. **WRITE ABOUT A THEME: INTERACTIONS** Animal life changed greatly during the Cambrian explosion, with some groups expanding in diversity and others declining. Write a short essay (100–150 words) interpreting these events as feedback regulation at the level of the biological community.
7. **SYNTHESIZE YOUR KNOWLEDGE**



This organism is an animal. What can you infer about its body structure and lifestyle (that might not be obvious from its appearance)? This animal has a protostome developmental pattern and a trochophore larva. Identify the major clades that this animal belongs to. Explain your selection, and describe when these clades originated and how they are related to one another.

For selected answers, see Appendix A.

33 An Introduction to Invertebrates

KEY CONCEPTS

33.1 Sponges are basal animals that lack tissues *p. 690*

33.2 Cnidarians are an ancient phylum of eumetazoans *p. 691*

33.3 Lophotrochozoans, a clade identified by molecular data, have the widest range of animal body forms *p. 694*

33.4 Ecdysozoans are the most species-rich animal group *p. 705*

33.5 Echinoderms and chordates are deuterostomes *p. 713*

Study Tip

Make a table: Invertebrates differ in how they obtain food, remove wastes, reproduce, and move throughout their habitat. As you read, summarize how members of the 11 phyla of invertebrates described in detail in this chapter solve these shared challenges of life.

Phylum	Feeding method	Waste removal	Repro-duction	Movement
Porifera	Filter feeders	Diffusion	Herma-phrodites	Sessile

Go to Mastering Biology

For Students (in eText and Study Area)
- Get Ready for Chapter 33
- Video: Echinoderm Tube Feet
- HHMI Animation: Coral Bleaching

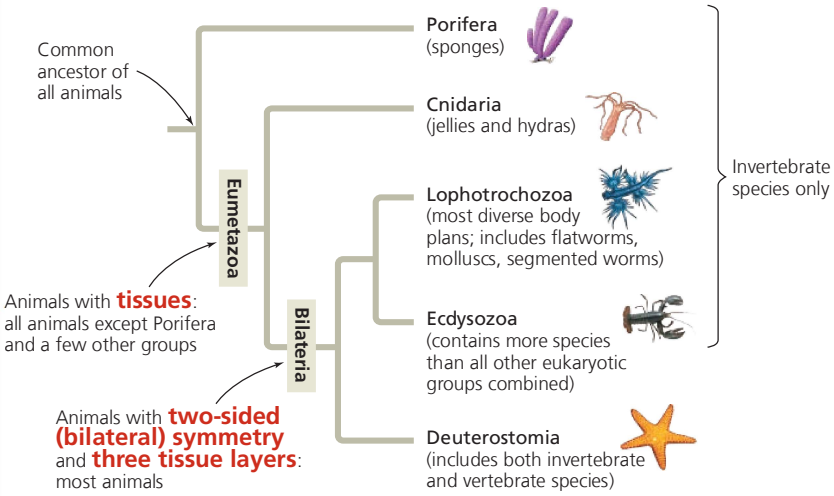
For Instructors to Assign (in Item Library)
- Tutorial: Ecdysozoans
- Scientific Skills Exercise: Understanding Experimental Design and Interpreting Data



Figure 33.1 The blue dragon (*Glaucus atlanticus*) has thin, finger-like structures that help it to float (upside down) on the sea's surface. It eats Portuguese men-of-war and absorbs their stinging cells, which it then uses to deliver a deadly sting of its own. The blue dragon is just one of more than a million species of invertebrates (animals without a backbone), which account for over 95% of animal species.

How can we make sense of the great number and morphological diversity of invertebrates?

Classifying invertebrate species into groups based on **evolutionary relationships**—as in this simplified phylogeny of all animals—helps us to understand the great diversity of invertebrate life.

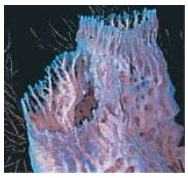


Invertebrates are animals that lack a backbone. They occupy almost every habitat on Earth, from the scalding water released by deep-sea hydrothermal vents to the frozen ground of Antarctica. Evolution in these varied environments has produced an immense diversity of forms, including species that are microscopic and species whose members can grow to 18 m long (1.5 times the length of a school bus). In this chapter, we'll take a tour of the invertebrates, using the phylogenetic tree in Figure 33.1 as a guide. **Figure 33.2** surveys 23 phyla as representatives of invertebrate diversity.

▼ Figure 33.2 Exploring Invertebrate Diversity

Kingdom Animalia encompasses 1.3 million known species, and estimates of the total number of species range as high as 10–20 million. Of the 23 phyla surveyed here, 13 are discussed more fully in this chapter, Chapter 32, or Chapter 34; cross-references are given at the end of their descriptions.

Porifera (5,500 species)



A sponge

Animals in this phylum are informally called sponges. Sponges are sessile animals that lack tissues. They live as filter feeders, trapping particles that pass through the internal channels of their body (see Concept 33.1).

Cnidaria (10,000 species)

Cnidarians include corals, jellies, and hydras. These animals have a diploblastic, radially symmetrical body plan that includes a gastrovascular cavity with a single opening that serves as both mouth and anus (see Concept 33.2).



A jelly

Acoela (400 species)

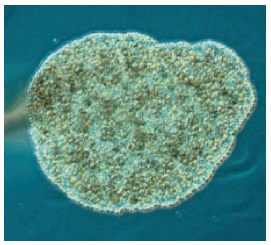


Acoela

Flatworms in this phylum have a simple nervous system and a saclike gut, and thus were once placed in phylum Platyhelminthes. Recent molecular analyses, however, indicate that Acoela is a separate lineage that diverged before the three main bilaterian clades (see Concept 32.4).

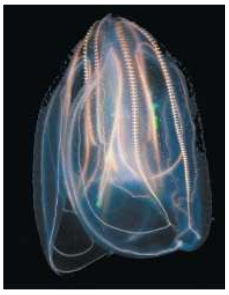
Placozoa (1 species)

The single known species in this phylum, *Trichoplax adhaerens*, doesn't look like an animal. It consists of a simple bilayer of a few thousand cells and reproduces by dividing into two individuals or by budding off many multicellular individuals. Placozoans are thought to be basal animals, but it is not yet known how they are related to Porifera, Cnidaria, and other early-diverging phyla.



A placozoan (LM) 0.5 mm

Ctenophora (100 species)

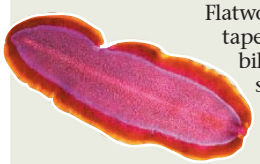


A ctenophore, or comb jelly

Ctenophores (comb jellies) are diploblastic and radially symmetrical like cnidarians, suggesting that both phyla diverged early from other animals. Comb jellies make up much of the ocean's plankton. They have eight "combs" of cilia that propel the animals through the water. When a small animal contacts the tentacles of some comb jellies, specialized cells burst open, covering the prey with sticky threads.

Lophotrochozoa

Platyhelminthes (20,000 species)



A marine flatworm

Flatworms in this phylum (including tapeworms, planarians, and flukes) have bilateral symmetry and a central nervous system that processes information from sensory structures. They have no body cavity or specialized organs for circulation (see Concept 33.3).

Syndermata (2,900 species)

This recently established phylum includes two groups formerly classified as separate phyla: the rotifers, microscopic animals with complex organ systems, and the acanthocephalans, highly modified parasites of vertebrates (see Concept 33.3).



A rotifer (LM)

Continued on next page

▼ Figure 33.2 (continued)

Ectoprocta (4,500 species)



Ectoprocts

Ectoprocts (also known as bryozoans) live as sessile colonies and are covered by a tough exoskeleton (see Concept 33.3).

Brachiopoda (335 species)



A brachiopod

Brachiopods, or lamp shells, may be easily mistaken for clams or other molluscs. However, most brachiopods have a unique stalk that anchors them to their substrate, as well as a crown of cilia called a lophophore (see Concept 33.3).

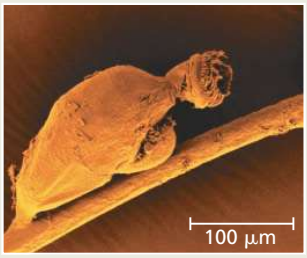
Gastrotricha (800 species)

Gastrotrichs are tiny worms whose ventral surface is covered with cilia, leading them to be called hairy bellies. Most species live on the bottoms of lakes or oceans, where they feed on small organisms and partially decayed organic matter. This individual has consumed algae, visible as the greenish material inside its gut.



A gastrotrich (differential interference contrast LM)

Cycliophora (1 species)



A cycliophoran (colorized SEM)

The only known cycliphoran species, *Symbion pandora*, was discovered in 1995 on the mouthparts of a lobster. This tiny creature has a unique body plan and a bizarre life cycle: Males impregnate females that are still developing in their mothers' bodies. The fertilized females escape, settle elsewhere on the lobster, and release their offspring.



A ribbon worm

Nemertea (900 species)

Also called ribbon worms, nemerteans swim through water or burrow in sand, extending a unique proboscis to capture prey. Nemerteans have a reduced coelom, so their bodies are relatively solid. They also have an alimentary canal and a closed circulatory system in which the blood is contained in vessels and hence is distinct from fluid in the body cavity.

Annelida (16,500 species)

Annelids, or segmented worms, are distinguished by their body segmentation. Earthworms are the most familiar annelids, but most annelids live in marine or freshwater habitats (see Concept 33.3).



Mollusca (100,000 species)

Molluscs (including snails, clams, squids, and octopuses) have a soft body that in many species is protected by a hard shell (see Concept 33.3).



An octopus

Ecdysozoa

Loricifera (10 species)

Loriciferans (from the Latin *lorica*, corset, and *ferre*, to bear) are tiny animals that inhabit sediments on the seafloor. A loriciferan can telescope its head, neck, and thorax in and out of the lorica, a pocket formed by six plates surrounding the abdomen. Though the natural history of loriciferans is mostly a mystery, at least some species likely eat bacteria.



A loriciferan (LM)

Priapula (16 species)



A priapulan

Priapulans are worms with a large, rounded proboscis at the anterior end. (They are named after Priapos, the Greek god of fertility, who was symbolized by a giant penis.) Ranging from 0.5 mm to 20 cm in length, most species burrow through seafloor sediments. Fossil evidence suggests that priapulans were among the major predators during the Cambrian period.

Onychophora (110 species)



An onychophoran

Onychophorans, also called velvet worms, originated during the Cambrian explosion (see Concept 25.3). Originally, they thrived in the ocean, but at some point they succeeded in colonizing land. Today they live only in humid forests. Onychophorans have fleshy antennae and several dozen pairs of saclike legs.

Nematoda (25,000 species)



A roundworm

Also called roundworms, nematodes are enormously abundant and diverse in the soil and in aquatic habitats; many species parasitize plants and animals. Their most distinctive feature is a tough cuticle that coats their body (see Concept 33.4).

Tardigrada (800 species)



Tardigrades (colorized SEM)

Tardigrades (from the Latin *tardus*, slow, and *gradus*, step) are sometimes called water bears for their overall shape and lumbering, bearlike gait. Most tardigrades are less than 0.5 mm in length. Some live in oceans or fresh water, while others live on plants or animals. Harsh conditions may cause tardigrades to enter a state of dormancy; while dormant, they can survive for days at temperatures as low as −200°C! A recent phylogenomic study found that over 15% of tardigrade genes entered their genome by horizontal gene transfer, the largest fraction known for any animal.



A spider (an arachnid)

Arthropoda (1,000,000 species)

The vast majority of known animal species, including insects, crustaceans, and arachnids, are arthropods. All arthropods have a segmented exoskeleton and jointed appendages (see Concept 33.4).

Deuterostomia

Hemichordata (85 species)

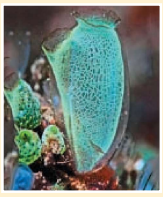


An acorn worm

Like echinoderms and chordates, hemichordates are members of the deuterostome clade (see Figure 32.11). Hemichordates share some traits with chordates, such as gill slits and a dorsal nerve cord. The largest group of hemichordates is the enteropneusts, or acorn worms. Acorn worms are marine and generally live buried in mud or under rocks; they may grow to more than 2 m in length.

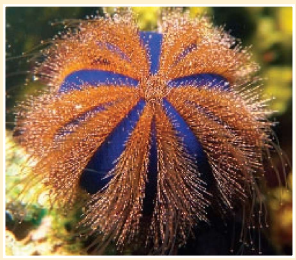
Chordata (60,000 species)

More than 90% of all known chordate species have backbones (and thus are vertebrates). However, the phylum Chordata also includes two groups of invertebrates: lancelets and tunicates. See Chapter 34 for a full discussion of this phylum.



A tunicate

Echinodermata (7,000 species)



A sea urchin

Echinoderms, such as sand dollars, sea stars, and sea urchins, are marine animals in the deuterostome clade that are bilaterally symmetrical as larvae but not as adults. They move and feed by using a network of internal canals to pump water to different parts of their body (see Concept 33.5).

CONCEPT 33.1

Sponges are basal animals that lack tissues



Animals in the phylum Porifera are known informally as sponges. Among the simplest of animals, sponges are sedentary and were mistaken for plants by the ancient Greeks. Most species are marine, and they range in size from a few millimeters to a few meters. Sponges are **filter feeders**: They filter out food particles suspended in the surrounding water as they draw it through their body, which in some species resembles a sac perforated with pores. Water is drawn through the pores into a central cavity, the **spongocoel**, and then flows out of the sponge through a larger opening called the **osculum** **(Figure 33.3)**. More complex sponges have folded body walls, and many contain branched water canals and several oscula.

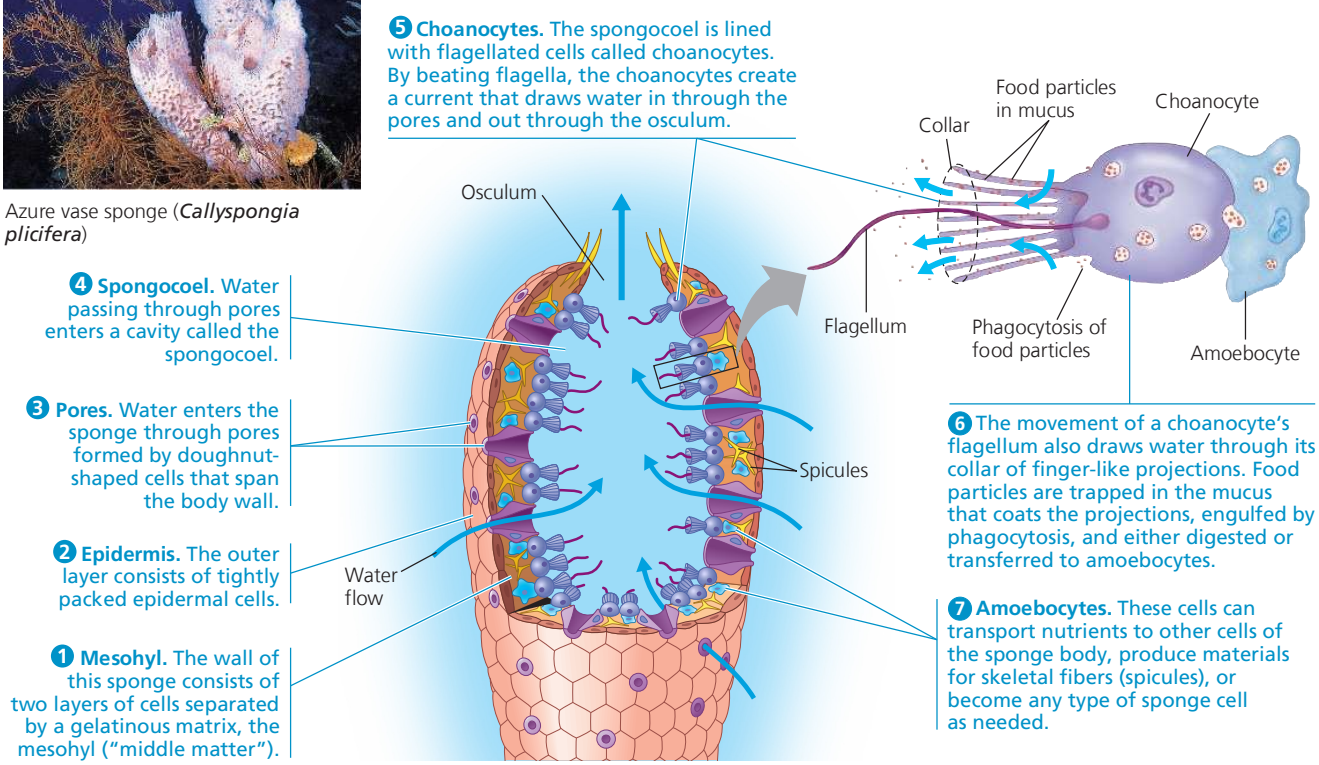
Sponges represent a lineage that diverged from other animals early in the history of the group; thus, they are said to be *basal animals*. Unlike nearly all other animals, sponges lack tissues, groups of similar cells that act as a functional unit as in muscle tissue and nervous tissue. However, the sponge body does contain several different cell types. For example, lining the interior of the spongocoel are flagellated **choanocytes**, or collar cells (named for the finger-like projections that form a "collar" around the flagellum). These cells engulf bacteria and other food particles by phagocytosis. The similarity between choanocytes and the cells of choanoflagellates supports molecular evidence indicating that animals and choanoflagellates are sister groups (see Figure 32.3).

The body of a sponge consists of two layers of cells separated by a gelatinous region called the **mesohyl**. Because both cell layers are in contact with water, processes such as gas exchange and waste removal can occur by diffusion across the membranes of these cells. Other tasks are performed by cells called **amoebocytes**, named for their use of pseudopodia. These cells move through the mesohyl and have many functions. For example, they take up food from the surrounding water and from choanocytes, digest it, and carry nutrients to other cells. Amoebocytes also manufacture tough skeletal fibers within the mesohyl. In some sponges, these fibers are sharp spicules made from calcium carbonate or silica. Other sponges produce more flexible fibers composed of a protein called spongin; you may have seen these pliant skeletons being sold as brown bath sponges. Finally, and perhaps most

▼ **Figure 33.3** **Anatomy of a sponge.** In the main diagram, portions of the front and back wall are cut away to show the sponge's internal structure.



Azure vase sponge (*Callyspongia plicifera*)



importantly, amoebocytes are *totipotent* (capable of becoming other types of sponge cells). This gives the sponge body remarkable flexibility, enabling it to adjust its shape in response to changes in its physical environment (such as the direction of water currents).

Most sponges are **hermaphrodites**, meaning that each individual functions as both male and female in sexual reproduction by producing sperm *and* eggs. Almost all sponges exhibit sequential hermaphroditism: They function first as one sex and then as the other. Cross-fertilization can result when sperm released into the water current by an individual functioning as a male is drawn into a neighboring individual that is functioning as a female. The resulting zygotes develop into flagellated, swimming larvae that disperse from the parent sponge. After settling on a suitable substrate, a larva develops into a sessile adult.

Sponges produce a variety of antibiotics and other defensive compounds, which hold promise for fighting human diseases. For example, a compound called cribrostatin isolated from marine sponges can kill both cancer cells and penicillin-resistant strains of the bacterium *Streptococcus*. Other sponge-derived compounds are also being tested as possible anticancer agents.

CONCEPT CHECK 33.1

1. Describe how sponges feed.
2. **WHAT IF?** Some molecular evidence suggests that the sister group of animals is not the choanoflagellates, but rather a group of parasitic protists, Mesomycetozoa. Given that these parasites lack collar cells, can this hypothesis be correct? Explain.

For suggested answers, see Appendix A.

CONCEPT 33.2

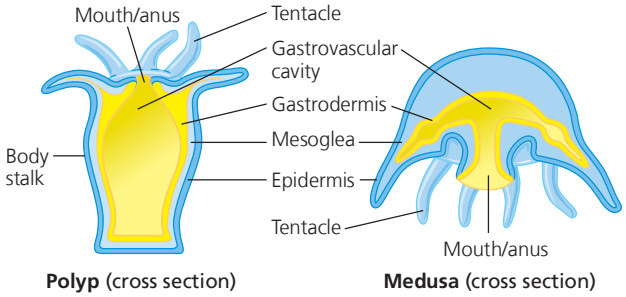
Cnidarians are an ancient phylum of eumetazoans



All animals except sponges and a few other groups are *eumetazoans* ("true animals"), members of a clade of animals with tissues. One of the first lineages to have diverged from others in this clade is the phylum Cnidaria, which originated about 680 million years ago according to DNA analyses. Cnidarians have diversified into a wide range of sessile and motile forms, including hydras, corals, and jellies (commonly called "jellyfish"). Yet most cnidarians still exhibit the relatively simple, diploblastic, radial body plan that existed in early members of the group some 560 million years ago.

The basic body plan of a cnidarian is a sac with a central digestive compartment, the **gastrovascular cavity**. A single opening to this cavity functions as both mouth and anus. There are two variations on this body plan: the largely sessile polyp and the more motile medusa **(Figure 33.4)**. **Polyps** are cylindrical forms that adhere to the substrate by the aboral end of their body (the end opposite the mouth) and extend their tentacles, waiting for prey. Examples of the polyp form include hydras and sea anemones. Although they are primarily sedentary, many polyps can move slowly across their substrate using muscles at the aboral end of their body. When threatened by a predator, some sea anemones can detach from the substrate and "swim" by bending their body column back and forth, or thrashing their tentacles. A **medusa** (plural, *medusae*) resembles a flattened, mouth-down version of the polyp. It moves freely in the water by a combination of passive drifting and contractions of its bell-shaped body. Medusae include free-swimming jellies. The tentacles of a jelly dangle from the oral surface, which points downward. Some cnidarians exist only as polyps or only as medusae; others have both a polyp stage and a medusa stage in their life cycle.

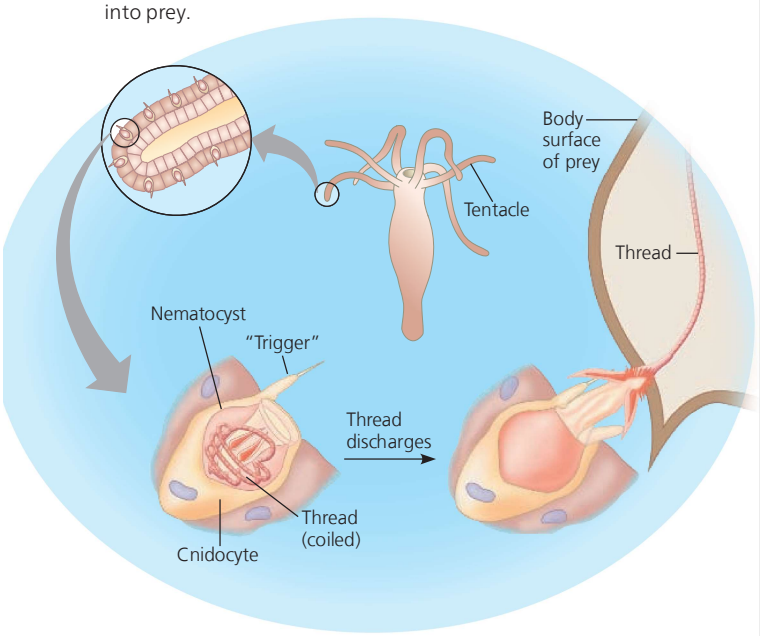
▼ Figure 33.4 Polyp and medusa forms of cnidarians. The body wall of a cnidarian has two layers of cells: an outer layer of epidermis (darker blue; derived from ectoderm) and an inner layer of gastrodermis (yellow; derived from endoderm). Digestion begins in the gastrovascular cavity and is completed inside food vacuoles in the gastrodermal cells. Sandwiched between the epidermis and gastrodermis is a gelatinous layer, the mesoglea.



Cnidarians are predators that often use tentacles arranged in a ring around their mouth to capture prey and push the food into their gastrovascular cavity, where digestion begins. Enzymes are secreted into the cavity, thus breaking down the prey into a nutrient-rich broth. Cells lining the cavity then absorb these nutrients and complete the digestive process; any undigested remains are expelled through the cnidarian's mouth/anus. The tentacles are armed with batteries of **cnidocytes**, cells unique to cnidarians that function in defense and prey capture. Cnidocytes contain *cnidae* (from the Greek *cnide*, nettle), capsule-like organelles that are capable of exploding outward and that give phylum Cnidaria its name **(Figure 33.5)**. Specialized cnidae called **nematocysts** contain a stinging thread that can penetrate the body surface of the cnidarian's prey. Other kinds of cnidae have long threads that stick to or entangle small prey that bump into the cnidarian's tentacles.

Contractile tissues and nerves occur in their simplest forms in cnidarians. Cells of the epidermis (outer layer) and

▼ Figure 33.5 A cnidocyte of a hydra. This type of cnidocyte contains a stinging capsule, the nematocyst, which contains a coiled thread. When a "trigger" is stimulated by touch or by certain chemicals, the thread shoots out, puncturing and injecting poison into prey.



gastrodermis (inner layer) have bundles of microfilaments arranged into contractile fibers. The gastrovascular cavity acts as a hydrostatic skeleton (see Concept 50.6) against which the contractile cells can work. When a cnidarian closes its mouth, the volume of the cavity is fixed, and contraction of selected cells causes the animal to change shape. Cnidarians have no brain. Instead, movements are coordinated by a noncentralized *nerve net* that is associated with sensory structures distributed around the body. Thus, even though it lacks a brain, the animal can detect and respond to stimuli from all directions.

Fossil and molecular evidence suggests that early in its evolutionary history, the phylum Cnidaria diverged into two major clades, Medusozoa and Anthozoa **(Figure 33.6)**.

Medusozoans

All cnidarians that produce a medusa are members of clade Medusozoa, a group that includes the *scyphozoans* (jellies) and *cubozoans* (box jellies) shown in Figure 33.6a, along with the *hydrozoans*. Most hydrozoans alternate between the polyp and medusa forms, as seen in the life cycle of *Obelia* **(Figure 33.7)**. The polyp stage, a colony of interconnected polyps in the case of *Obelia*, is more conspicuous than the medusa. Hydras, among the few cnidarians found in fresh water, are also unusual hydrozoans in that they exist only in polyp form.

Unlike hydrozoans, most scyphozoans and cubozoans spend the majority of their life cycles in the medusa stage. Coastal scyphozoans, for example, often have a brief polyp stage during their life cycle, whereas those that live in the open ocean generally lack the polyp stage altogether. As their name (which means "cube animals") suggests, cubozoans have a box-shaped medusa stage. Most cubozoans live in tropical oceans and are equipped with highly toxic cnidocytes. For example, the sea wasp (*Chironex fleckeri*), a cubozoan that lives off the coast of northern Australia, is one of the deadliest organisms known: Its sting causes intense pain and can lead to respiratory failure, cardiac arrest, and death within minutes.

▼ Figure 33.6 Cnidarians.

(a) Medusozoans



Many scyphozoans (jellies) are bioluminescent. Food captured by nematocyst-bearing tentacles is transferred to specialized oral arms for transport to the mouth.



This cubozoan, a sea wasp, produces a poison that can subdue fish, crustaceans (as seen here), and other large prey. The poison is more potent than cobra venom.

(b) Anthozoans



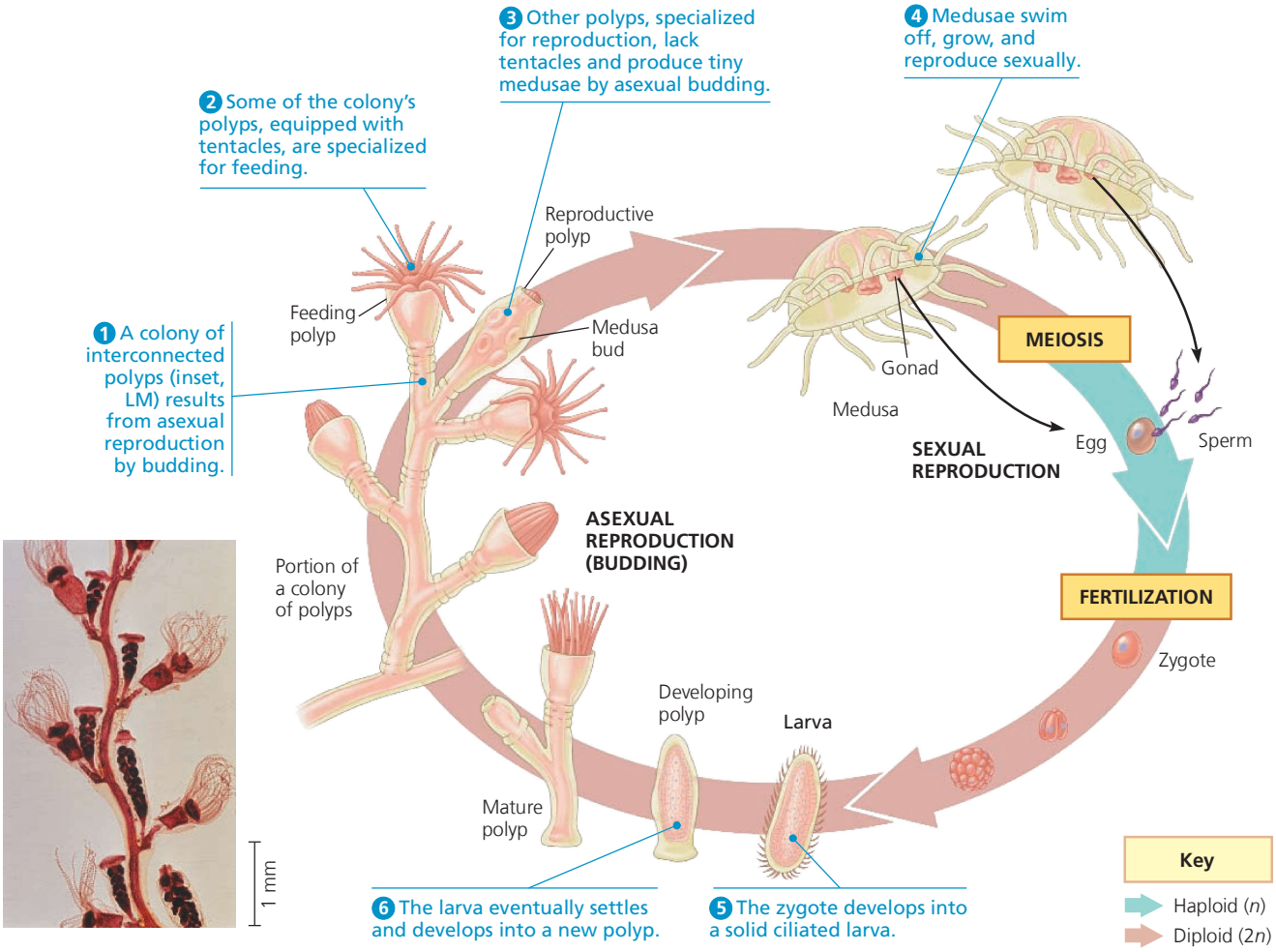
Sea anemones and other anthozoans exist only as polyps. Many anthozoans form symbiotic relationships with photosynthetic algae.



These star corals live as colonies of polyps. Their soft bodies are enclosed at the base by a hard exoskeleton.

Mastering Biology
Video: Jelly Swimming • Video: Hydra Eating *Daphnia*

▼ Figure 33.7 The life cycle of the hydrozoan *Obelia*. The polyp is asexual, and the medusa is sexual, releasing eggs and sperm. These two stages alternate, one producing the other.



MAKE CONNECTIONS *Compare and contrast the* Obelia *life cycle to the life cycles in Figure 13.6. Which life cycle in that figure is most similar to that of* Obelia*? Explain. (See also Figure 29.5.)*

Anthozoans

Sea anemones and corals belong to the clade Anthozoa (see Figure 33.6b). These cnidarians occur only as polyps. Corals live as solitary or colonial forms, often forming symbioses with algae. Many species secrete a hard **exoskeleton** (external skeleton) of calcium carbonate. Each polyp generation builds on the skeletal remains of earlier generations, constructing rocklike reefs with shapes characteristic of their species. These skeletons are what we usually think of as coral.

Coral reefs are to tropical seas what rain forests are to tropical land areas: They provide habitat for many other species. Unfortunately, these reefs are being destroyed at an alarming rate. Pollution, overharvesting, and ocean acidification (see Figure 3.12) are major threats. Climate change is also contributing to their demise by raising seawater temperatures above the range in which corals thrive (see Concept 56.4).

Mastering Biology HHMI Animation: Coral Bleaching

CONCEPT CHECK 33.2

1. Compare and contrast the polyp and medusa forms of cnidarians.
2. **VISUAL SKILLS** Use the cnidarian life cycle diagram in Figure 33.7 to determine the ploidy of a feeding polyp and of a medusa.
3. **MAKE CONNECTIONS** Many new animal body plans emerged during and after the Cambrian explosion. In contrast, cnidarians today retain the same diploblastic, radial body plan found in cnidarians 560 million years ago. Are cnidarians therefore less successful or less "highly evolved" than other animal groups? Explain. (See Concepts 25.3 and 25.6.)

For suggested answers, see Appendix A.

CONCEPT 33.3

Lophotrochozoans, a clade identified by molecular data, have the widest range of animal body forms



The vast majority of animal species belong to the clade Bilateria, whose members exhibit bilateral symmetry and are triploblastic (see Concept 32.3). Most bilaterians also have a digestive tract with two openings (a mouth and an anus) and a body cavity (a coelom or hemocoel; see Figure 32.9). Recent DNA analyses suggest that the common ancestor of living bilaterians lived about 670 million years ago. To date, however, the oldest fossil that is widely accepted as a bilaterian is of *Kimberella*, a mollusc (or close relative) that lived 560 million years ago (see Figure 32.5b). Many other bilaterian groups first appeared in the fossil record during the Cambrian explosion (535 to 525 million years ago).

Molecular evidence suggests that today there are three major clades of bilaterally symmetrical animals: Lophotrochozoa, Ecdysozoa, and Deuterostomia. This section will focus on the first of these clades, the lophotrochozoans. Concepts 33.4 and 33.5 will explore the other two clades.

Although the clade Lophotrochozoa was identified by molecular data, its name comes from features found in some of its members. Some lophotrochozoans develop a structure called a *lophophore*, a crown of ciliated tentacles that functions in feeding, while others go through a distinctive stage called the *trochophore larva* (see Figure 32.12). Other members of the group have neither of these features. Few other unique morphological features are widely shared within the group—in fact, the lophotrochozoans are the most diverse bilaterian clade in terms of body plan. This diversity in form is reflected in the number of phyla classified in the group: Lophotrochozoa includes 18 phyla, more than twice the number in any other clade of bilaterians.

We'll now introduce six of the diverse lophotrochozoan phyla: the flatworms, rotifers and acanthocephalans, ectoprocts, brachiopods, molluscs, and annelids.

Flatworms

Flatworms (phylum Platyhelminthes) live in marine, freshwater, and damp terrestrial habitats. In addition to free-living species, flatworms include many parasitic species, such as flukes and tapeworms. Flatworms are so named because they have thin bodies that are flattened dorsoventrally (between the dorsal and ventral surfaces); the word *platyhelminth* means "flat worm." (Note that *worm* is not a formal scientific name but rather refers to animals with long, thin bodies.) The smallest flatworms are nearly microscopic free-living species, while some tapeworms are more than 20 m long.

Although flatworms are triploblastic, they lack a body cavity. Their flat shape increases their surface area, placing all their cells close to water in the surrounding environment or in their gut. Because of this proximity to water, gas exchange and the elimination of nitrogenous waste (ammonia) can occur by diffusion across the body surface. As shown in **Figure 33.8**, a flat shape is one of several structural features that maximize surface area and have arisen (by convergent evolution) in different groups of animals and other organisms.

As you might expect since all their cells are close to water, flatworms have no organs specialized for gas exchange, and their relatively simple excretory apparatus functions mainly to maintain osmotic balance with their surroundings. This apparatus consists of **protonephridia**, networks of tubules with ciliated structures called *flame bulbs* that pull fluid through branched ducts opening to the outside (see Figure 44.8). Most flatworms have a gastrovascular cavity with only one opening. Though flatworms lack a circulatory system, the fine branches of the gastrovascular cavity distribute food directly to the animal's cells.

Early in their evolutionary history, flatworms separated into two lineages, Catenulida and Rhabditophora. Catenulida is a small clade of about 100 flatworm species, most of which live in freshwater habitats. Catenulids typically reproduce asexually by budding at their posterior end. The offspring often produce their own buds before detaching from the parent, thereby forming a chain of two to four genetically identical individuals—hence their informal name, "chain worms."

The other ancient flatworm lineage, Rhabditophora, is a diverse clade of about 20,000 freshwater and marine species, one example of which is shown in Figure 33.8. We'll explore the rhabditophorans in more detail, focusing on free-living and parasitic members of this clade.

Free-Living Species

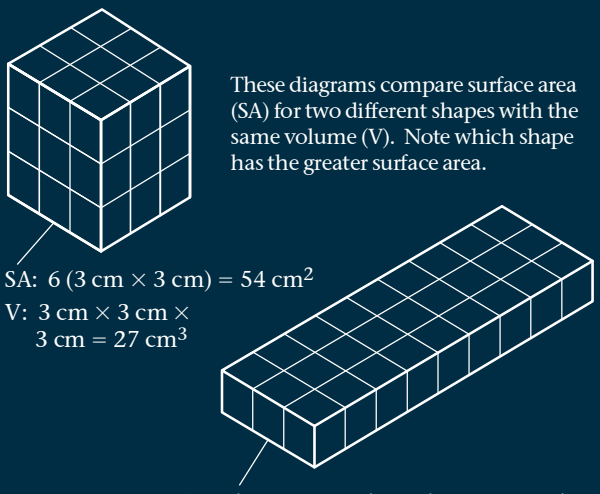
Free-living rhabditophorans are important as predators and scavengers in a wide range of freshwater and marine habitats. The best-known members of this group are freshwater species in the genus *Dugesia*, commonly called **planarians**. Abundant in unpolluted ponds and streams, planarians prey on smaller animals or feed on dead animals. They move by using cilia on their ventral surface, gliding along a film of mucus they secrete. Some other rhabditophorans also use their muscles to swim through water with an undulating motion.

A planarian's head features a pair of light-sensitive eyespots as well as lateral flaps that function mainly to detect specific chemicals. The planarian nervous system is more complex and centralized than the nerve nets of cnidarians

▼ **Figure 33.8**

MAKE CONNECTIONS

Maximizing Surface Area



These diagrams compare surface area (SA) for two different shapes with the same volume (V). Note which shape has the greater surface area.

In general, the amount of metabolic or chemical activity a cell or organism can carry out is proportional to its mass or volume. Maximizing metabolic rate, however, requires the efficient uptake of energy and raw materials, such as nutrients and oxygen, as well as the effective disposal of waste products. For large cells, plants, and animals, these exchange processes have the potential to be limiting due to simple geometry. When a cell or organism grows without changing shape, its volume increases more rapidly than its surface area (see Figure 6.7). As a result, there is proportionately less surface area over which exchange processes can occur. The challenge posed by the relationship between surface area and volume occurs in diverse contexts and organisms, but the evolutionary adaptations that meet this challenge are similar. Structures that maximize surface area through branching, flattening, folding, and projections have an essential role in biological systems.

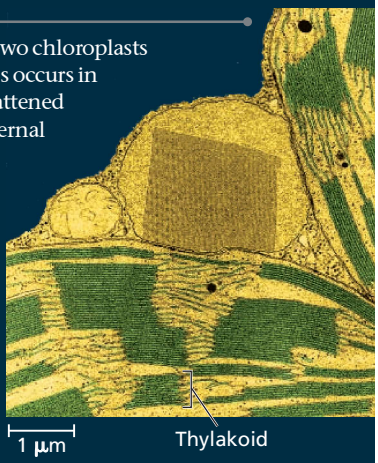
Branching

Water uptake relies on passive diffusion. The highly branched filaments of a fungal mycelium increase the surface area across which water and minerals can be absorbed from the environment. (See Figure 31.2.)



Folding

This TEM shows portions of two chloroplasts in a plant leaf. Photosynthesis occurs in chloroplasts, which have a flattened and interconnected set of internal membranes called thylakoid membranes. The foldings of the thylakoid membranes increase their surface area, enhancing the exposure to light and thus increasing the rate of photosynthesis. (See Figure 10.4.)



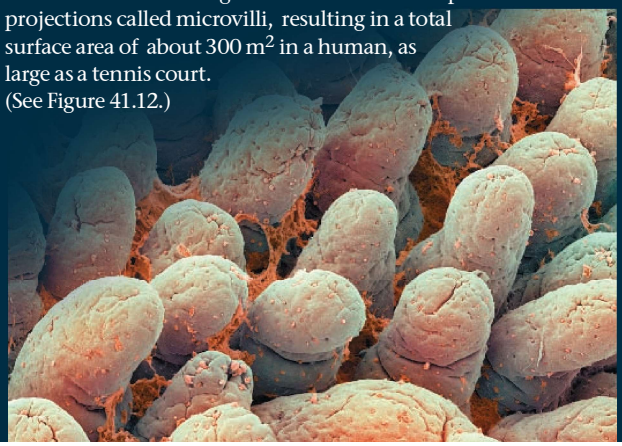
Flattening

By having a body that is only a few cells thick, an organism such as this flatworm can use its entire body surface for exchange. (See Figure 40.3)



Projections

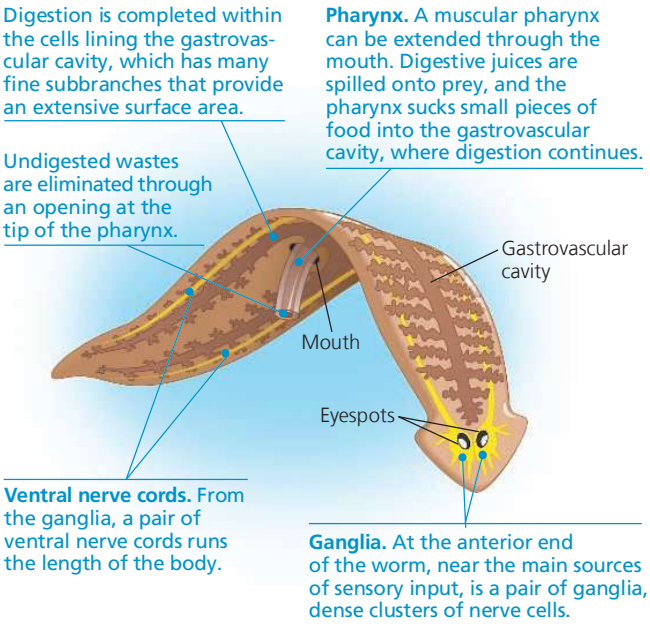
In vertebrates, the small intestine is lined with finger-like projections called villi that absorb nutrients released by the digestion of food. Each of the villi shown here is covered with large numbers of microscopic projections called microvilli, resulting in a total surface area of about 300 m^2 in a human, as large as a tennis court. (See Figure 41.12.)



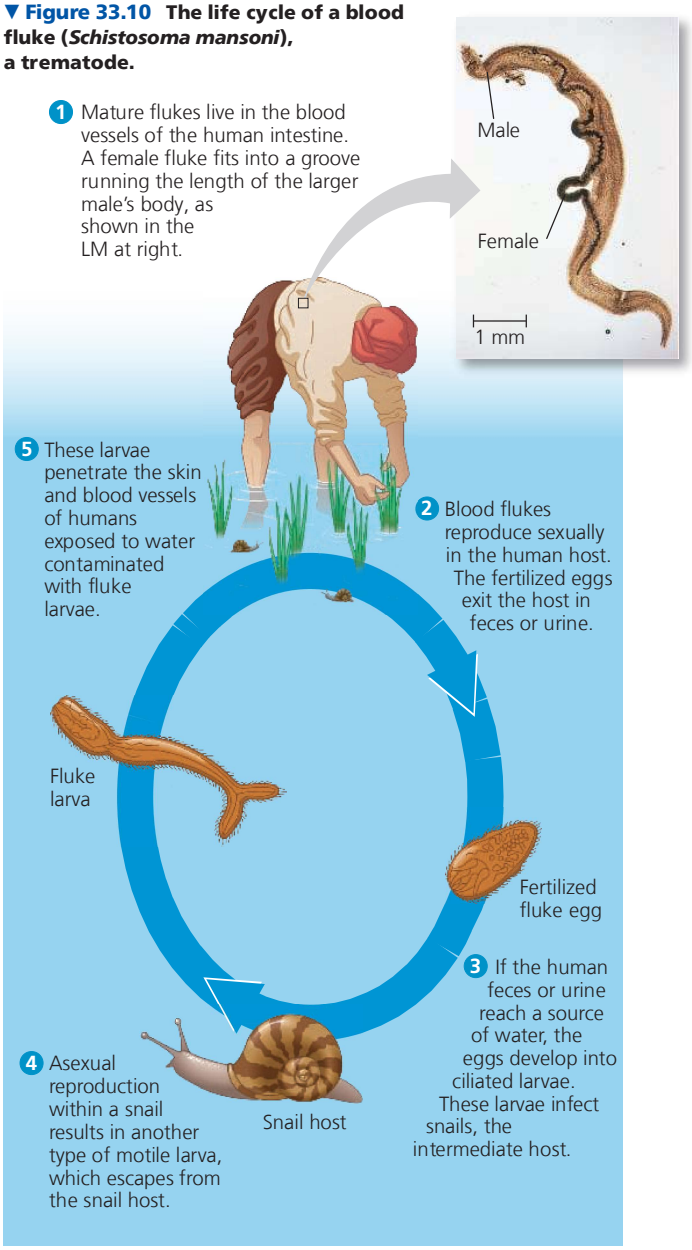
MAKE CONNECTIONS

Find other examples of flattening, folding, branching, and projections (see Chapters 6, 9, 35, and 42). How is maximizing surface area important to the structure's function in each example?

▼ Figure 33.9 Anatomy of a planarian.



▼ Figure 33.10 The life cycle of a blood fluke (*Schistosoma mansoni*), a trematode.



WHAT IF? *Snails eat algae, whose growth is stimulated by nutrients found in fertilizer. How would the contamination of irrigation water with fertilizer likely affect the occurrence of schistosomiasis? Explain.*

(Figure 33.9). Experiments have shown that planarians can learn to modify their responses to stimuli.

Some planarians can reproduce asexually through fission. The parent constricts roughly in the middle of its body, separating into a head end and a tail end; each end then regenerates the missing parts. Sexual reproduction also occurs. Planarians are hermaphrodites, and copulating mates typically cross-fertilize each other.

Parasitic Species

More than half of the known species of rhabditophorans live as parasites in or on other animals. Many have suckers that attach to the internal organs or outer surfaces of the host animal. In most species, a tough covering helps protect the parasites within their hosts. We'll discuss two ecologically and economically important subgroups of parasitic rhabditophorans, the trematodes and the tapeworms.

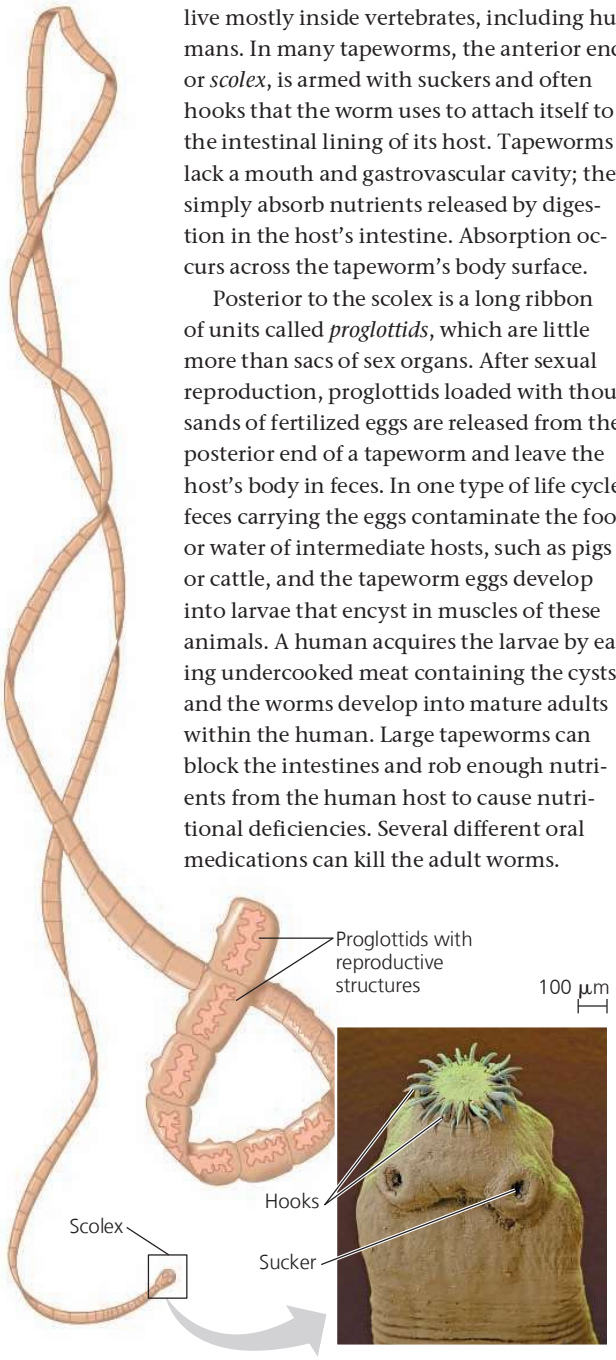
Trematodes As a group, trematodes parasitize a wide range of hosts, and most species have complex life cycles with alternating sexual and asexual stages. Many trematodes require an intermediate host in which larvae develop before infecting the final host (usually a vertebrate), where the adult worms live. For example, various trematodes that parasitize humans spend part of their lives in snail hosts **(Figure 33.10)**. Around the world, about 200 million people are infected with trematodes called blood flukes (*Schistosoma*) and suffer from schistosomiasis, a disease whose symptoms include pain, anemia, and diarrhea.

Living within more than one kind of host puts demands on trematodes that free-living animals don't face. A blood fluke, for instance, must evade the immune systems of both snails and humans. By mimicking the surface proteins of its hosts, the blood fluke creates a partial immunological camouflage for itself. It also releases molecules that manipulate the hosts' immune systems into tolerating the parasite's existence. These defenses are so effective that individual blood flukes can survive in humans for more than 40 years.

Tapeworms The tapeworms are a second large and diverse group of parasitic rhabditophorans **(Figure 33.11)**. The adults

live mostly inside vertebrates, including humans. In many tapeworms, the anterior end, or *scolex*, is armed with suckers and often hooks that the worm uses to attach itself to the intestinal lining of its host. Tapeworms lack a mouth and gastrovascular cavity; they simply absorb nutrients released by digestion in the host's intestine. Absorption occurs across the tapeworm's body surface.

Posterior to the scolex is a long ribbon of units called *proglottids*, which are little more than sacs of sex organs. After sexual reproduction, proglottids loaded with thousands of fertilized eggs are released from the posterior end of a tapeworm and leave the host's body in feces. In one type of life cycle, feces carrying the eggs contaminate the food or water of intermediate hosts, such as pigs or cattle, and the tapeworm eggs develop into larvae that encyst in muscles of these animals. A human acquires the larvae by eating undercooked meat containing the cysts, and the worms develop into mature adults within the human. Large tapeworms can block the intestines and rob enough nutrients from the human host to cause nutritional deficiencies. Several different oral medications can kill the adult worms.

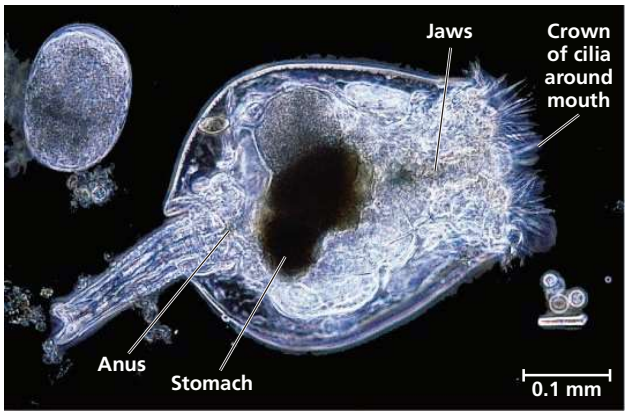


▲ **Figure 33.11** **Anatomy of a tapeworm.** The inset shows a close-up of the scolex (colorized SEM).

Rotifers and Acanthocephalans

Recent phylogenetic analyses have shown that two traditional animal phyla, the rotifers (former phylum Rotifera) and the acanthocephalans (former phylum Acanthocephala), should be combined into a single phylum, Syndermata. Each of the two groups has distinctive characteristics.

▼ **Figure 33.12** **A rotifer.** Although smaller than many unicellular protists, rotifers are multicellular and have specialized organ systems (LM).



Rotifers

There are roughly 1,800 species of rotifers, tiny animals that inhabit freshwater, marine, and damp soil habitats. Ranging in size from about 50 µm to 2 mm, rotifers are smaller than many protists but nevertheless are multicellular and have specialized organ systems **(Figure 33.12)**. In contrast to cnidarians and flatworms, which have a gastrovascular cavity, rotifers have an **alimentary canal**, a digestive tube with two openings, a mouth and an anus. Internal organs lie within the *hemocoel* (see Figure 32.9b). Fluid in the hemocoel serves as a hydrostatic skeleton. Movement of a rotifer's body distributes the fluid throughout the body, circulating nutrients.

The word *rotifer* is derived from the Latin meaning "wheel-bearer," a reference to the crown of cilia that draws a vortex of water into the mouth. Posterior to the mouth, rotifers have jaws called trophi that grind up food, mostly microorganisms suspended in the water. Digestion is then completed farther along the alimentary canal. Most other bilaterians also have an alimentary canal, which enables the stepwise digestion of a wide range of food particles.

Rotifers exhibit some unusual forms of reproduction. Some species consist only of females that produce more females from unfertilized eggs, a type of asexual reproduction called **parthenogenesis**. Some other invertebrates (for example, aphids and some bees) and even some vertebrates (for example, some lizards and some fishes) can also reproduce in this way. In addition to being able to produce females by parthenogenesis, some rotifers can also reproduce sexually under certain conditions, such as high levels of crowding. The resulting embryos can remain dormant for years. Once they break dormancy, the embryos develop into another generation of females that reproduce asexually.

It is puzzling that many rotifer species persist without males. The vast majority of animals and plants reproduce sexually at least some of the time, and sexual

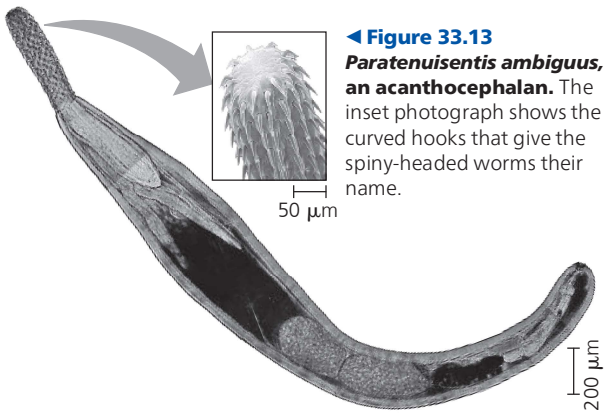
reproduction has certain advantages over asexual reproduction (see Concept 46.1). For example, species that reproduce asexually tend to accumulate harmful mutations in their genomes faster than sexually reproducing species. As a result, asexual species should experience higher rates of extinction.

Seeking to understand how they persist without males, researchers have been studying a clade of asexual rotifers named Bdelloidea. Some 360 species of bdelloid rotifers are known, and all of them reproduce by parthenogenesis without any males. Paleontologists have discovered bdelloid rotifers preserved in 35-million-year-old amber, and the morphology of these fossils resembles only the female form, with no evidence of males. Molecular clock analyses indicate that bdelloids have been asexual for over 50 million years. While it appears that they do not reproduce sexually, bdelloid rotifers may be able to generate genetic diversity in other ways. For example, bdelloids can tolerate very high levels of desiccation. When conditions improve and their cells rehydrate, DNA from other species enters their cells through cracks in the plasma membrane. Recent evidence suggests that this foreign DNA can be incorporated into the bdelloids' genome, thereby leading to increased genetic diversity.

Acanthocephalans

Acanthocephalans (1,100 species) are sexually reproducing parasites of vertebrates that lack a complete digestive tract and usually are less than 20 cm long. They are commonly called spiny-headed worms because of the curved hooks on the proboscis at the anterior end of their body **(Figure 33.13)**. Acanthocephalans are triploblastic and, like rotifers, they have a hemocoel. Recent studies have shown that acanthocephalans originated from within the group traditionally known as Rotifera. In particular, rotifers in the genus *Seison* share a more recent common ancestor with acanthocephalans than they do with other rotifers, making the acanthocephalans a group of highly modified "rotifers."

All acanthocephalans are parasites that have complex life cycles with two or more hosts. Some species manipulate the behavior of their intermediate hosts (generally arthropods) in ways that increase their chances of reaching their final hosts (generally vertebrates). For example, acanthocephalans that infect New Zealand mud crabs cause their hosts to move to more visible areas on the beach, where the crabs are more likely to be eaten by birds, the worms' final hosts.



◀ Figure 33.13 ***Paratenuisentis ambiguus*, an acanthocephalan.** The inset photograph shows the curved hooks that give the spiny-headed worms their name.

Ectoprocts and Brachiopods

Bilaterians in the phyla Ectoprocta and Brachiopoda have a *lophophore*, a crown of ciliated tentacles around their mouth (see Figure 32.12a). As the cilia draw water toward the mouth, the tentacles trap suspended food particles. Other similarities, such as a U-shaped alimentary canal and the absence of a distinct head, reflect these organisms' sessile existence. In contrast to flatworms, which lack a body cavity, and rotifers, which have a hemocoel, ectoprocts and brachiopods have a coelom (see Figure 32.9a).

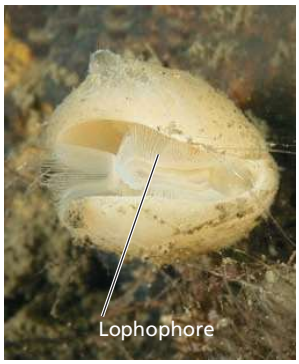
Ectoprocts (from the Greek *ecto*, outside, and *procta*, anus) are colonial animals that superficially resemble clumps of moss. (In fact, their common name, bryozoans, means "moss animals.") In most species, the colony is encased in a hard exoskeleton studded with pores through which the lophophores extend **(Figure 33.14a)**. Most ectoproct species live in the sea, where they are among the most widespread and numerous sessile animals. Several species are important reef builders. Ectoprocts also live in lakes and rivers. Colonies of the freshwater ectoproct *Pectinatella magnifica* grow on submerged sticks or rocks and can grow into a gelatinous, ball-shaped mass more than 10 cm across.

Brachiopods, or lamp shells, superficially resemble clams and other hinge-shelled molluscs, but the two halves of the brachiopod shell are dorsal and ventral rather than lateral, as in clams **(Figure 33.14b)**. All brachiopods are marine. Most live attached to the seafloor by a stalk, opening their shell slightly to allow water to flow through the lophophore. The living brachiopods are remnants of a much richer past that included

▼ Figure 33.14 Ectoprocts and brachiopods.



(a) Ectoprocts, such as this creeping bryozoan (*Plumatella repens*), are colonial.



(b) Brachiopods, such as this lampshell (*Terebratulina retusa*), have a hinged shell. The two parts of the shell are dorsal and ventral.

30,000 species in the Paleozoic and Mesozoic eras. Some living brachiopods, such as those in the genus *Lingula*, appear nearly identical to fossils of species that lived 400 million years ago.

Molluscs

Snails and slugs, oysters and clams, and octopuses and squids are all molluscs (phylum Mollusca). There are over 100,000 known species, making them the second most diverse phylum of animals (after the arthropods, discussed later). Although the majority of molluscs are marine, roughly 8,000 species inhabit fresh water, and 28,000 species of snails and slugs live on land. All molluscs are soft-bodied, and most secrete a hard protective shell made of calcium carbonate. Slugs, squids, and octopuses have a reduced internal shell or have lost their shell completely during their evolution.

Despite their apparent differences, all molluscs have a similar body plan **(Figure 33.15)**. The primary body cavity is a hemocoel, but they also have a reduced coelom. The body of a mollusc has three main parts: a muscular **foot**, usually used for movement; a **visceral mass** containing most of the internal organs; and a **mantle**, a fold of tissue that drapes over the visceral mass and secretes a shell (if one is present). In many molluscs, the mantle extends beyond the visceral mass, producing a water-filled chamber, the **mantle cavity**, which houses the gills, anus, and excretory pores. Many molluscs feed by using a straplike organ called a **radula** to scrape up food.

Most molluscs have separate sexes, and their gonads (ovaries or testes) are located in the visceral mass. Many snails, however, are hermaphrodites. The life cycle of many marine molluscs includes a ciliated larval stage, the trochophore (see Figure 32.12b), which is also characteristic of marine annelids (segmented worms) and some other lophotrochozoans.

The basic body plan of molluscs has evolved in various ways in the phylum's eight major clades. We'll examine four of those clades here: Polyplacophora (chitons), Gastropoda (snails and slugs), Bivalvia (clams, oysters, and other bivalves), and Cephalopoda (squids, octopuses, cuttlefishes, and chambered nautiluses). We will then focus on threats facing some groups of molluscs.

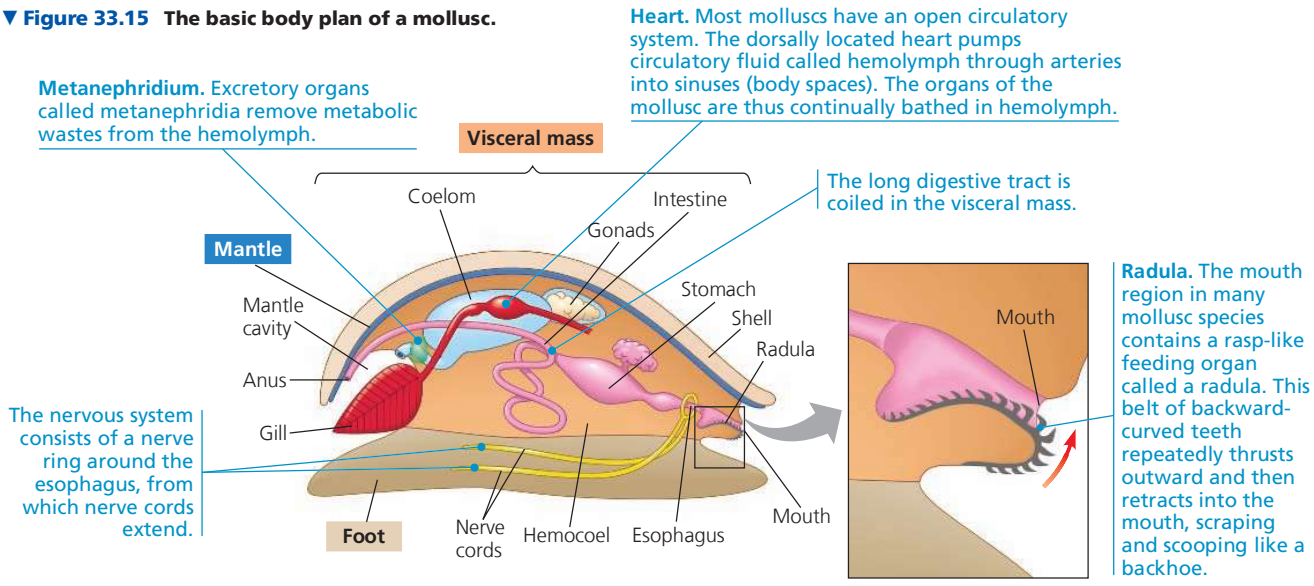
Chitons

Chitons have an oval-shaped body and a shell composed of eight dorsal plates **(Figure 33.16)**. The chiton's body itself, however, is unsegmented. You can find these marine animals clinging to rocks along the shore during low tide. If you try to dislodge a chiton by hand, you will be surprised at how well its foot, acting as a suction cup, grips the rock. A chiton can also use its foot to creep slowly over the rock surface. Chitons use their radula to scrape algae off the rock surface.

▼ Figure 33.16 A chiton. Note the eight-plate shell characteristic of molluscs in the clade Polyplacophora.



▼ Figure 33.15 The basic body plan of a mollusc.



Gastropods

About three-quarters of all living species of molluscs are gastropods **(Figure 33.17)**. Most gastropods are marine, but there are also freshwater species. Still other gastropods have adapted to life on land, where snails and slugs thrive in habitats ranging from deserts to rain forests.

Gastropods move literally at a snail's pace by a rippling motion of their foot or by means of cilia—a slow process that can leave them vulnerable to attack. Most gastropods have a single, spiraled shell into which the animal can retreat when threatened. The shell, which is secreted by glands at the edge of the mantle, has several functions, including protecting the animal's soft body from injury and dehydration. One of its most important roles is as a defense against predators, as is demonstrated by comparing populations with different histories of predation (see the **Scientific Skills Exercise**). As they move slowly about, most gastropods use their radula to graze on algae or plants. Several groups, however, are predators, and their radula has become modified for boring holes in the shells of other molluscs or for tearing apart prey. In the cone snails, the teeth of the radula act as poison darts that are used to subdue prey.



(a) A land snail



(b) A sea slug. Nudibranchs, or sea slugs, lost their shell during their evolution.

▲ Figure 33.17
Gastropods. The many species of gastropods have colonized terrestrial as well as aquatic environments.

Scientific Skills Exercise

Understanding Experimental Design and Interpreting Data

Is There Evidence of Selection for Defensive Adaptations in Mollusc Populations Exposed to Predators? The fossil record shows that historically, increased risk to prey species from predators is often accompanied by increased incidence and expression of prey defenses. Researchers tested whether populations of the predatory European green crab (*Carcinus maenas*) have exerted similar selective pressures on its gastropod prey, the flat periwinkle (*Littorina obtusata*). Periwinkles from southern sites in the Gulf of Maine have experienced predation by European green crabs for over 100 generations, at about one generation per year. Periwinkles from northern sites in the Gulf have been interacting with the invasive green crabs for relatively few generations, as the invasive crabs spread to the northern Gulf comparatively recently.

▼ A periwinkle

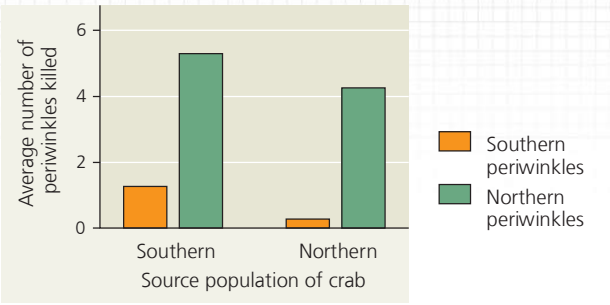


Previous research shows that (1) periwinkle shells recently collected from the Gulf are thicker than those collected in the late 1800s, and (2) periwinkle populations from southern sites have thicker shells than periwinkle populations from northern sites. In this exercise, you'll interpret the design and results of the researchers' experiment studying the rates of predation by crabs on periwinkles from northern and southern populations.

How the Experiment Was Done The researchers collected periwinkles and crabs from sites in the northern and southern Gulf of Maine, separated by 450 km of coastline. A single crab was placed in a cage with eight periwinkles of different sizes. After three days, researchers assessed the fate of the eight periwinkles. Four different treatments were set up, with crabs from northern or southern populations offered periwinkles from northern and southern populations. All crabs were of similar size and included equal numbers of males and females. Each experimental treatment was tested 12 to 14 times.

In a second part of the experiment, the bodies of periwinkles from northern and southern populations were removed from their shells and presented to crabs from northern and southern populations.

Data from the Experiment



Data from R. Rochette et al., Interaction between an invasive decapod and a native gastropod: Predator foraging tactics and prey architectural defenses, *Marine Ecology Progress Series* 330:179–188 (2007).

When the researchers presented the crabs with unshelled periwinkles, all the unshelled periwinkles were consumed in less than an hour.

INTERPRET THE DATA

1. What hypotheses were the researchers testing in this study? What are the independent variables? What are the dependent variables?
2. Why did the research team set up four different treatments?
3. Why did researchers present unshelled periwinkles to the crabs? What do the results of this part of the experiment indicate?
4. Summarize the results of the experiment. Do these results support the hypothesis you identified in question 1? Explain.
5. Suggest how natural selection may have affected populations of flat periwinkles in the southern Gulf of Maine over the last 100 years.

Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology**.

Many gastropods have a head with eyes at the tips of tentacles. Terrestrial snails lack the gills typical of most aquatic gastropods. Instead, the lining of their mantle cavity functions as a lung, exchanging respiratory gases with the air.

Bivalves

The molluscs of the clade Bivalvia are all aquatic and include many species of clams, oysters, mussels, and scallops. Bivalves have a shell divided into two halves **(Figure 33.18)**. The halves are hinged, and powerful adductor muscles draw them tightly together to protect the animal's soft body. Bivalves have no distinct head, and the radula has been lost. Some bivalves have eyes and sensory tentacles along the outer edge of their mantle.

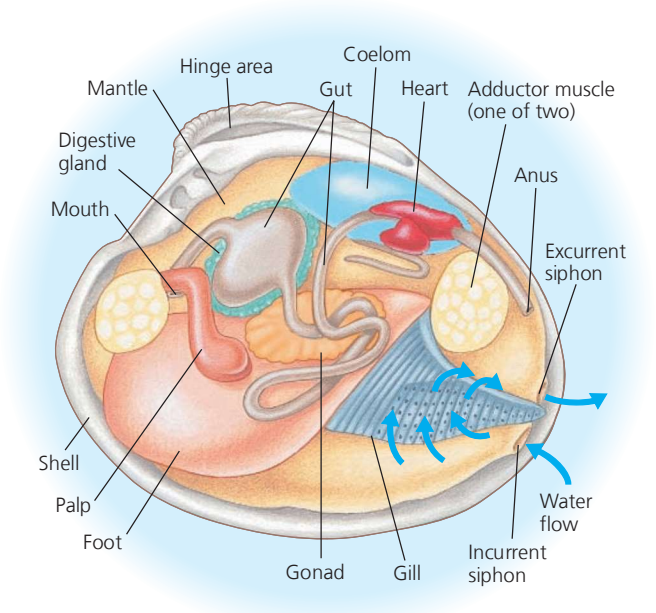
The gills of bivalves are used for feeding as well as gas exchange in most species **(Figure 33.19)**. Most bivalves are suspension feeders. They trap small food particles in mucus that coats their gills, and cilia then convey those particles to the mouth. Water enters the mantle cavity through an incurrent siphon, passes over the gills, and then exits the mantle cavity through an excurrent siphon.

Most bivalves lead sedentary lives, a characteristic suited to suspension feeding. Mussels secrete strong threads that tether them to rocks, docks, boats, and the shells of other animals. However, clams can pull themselves into the sand or mud, using their muscular foot for an anchor, and scallops can skitter along the seafloor by flapping their shells, rather like the mechanical false teeth sold in novelty shops.

▼ Figure 33.18 A bivalve. This scallop has many eyes (dark blue spots) lining each half of its hinged shell.



▼ Figure 33.19 Anatomy of a clam. Food particles suspended in water that enters through the incurrent siphon are collected by the gills and passed via cilia and the palps to the mouth.



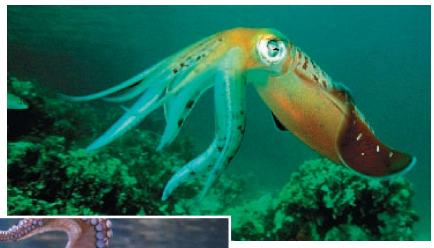
Cephalopods

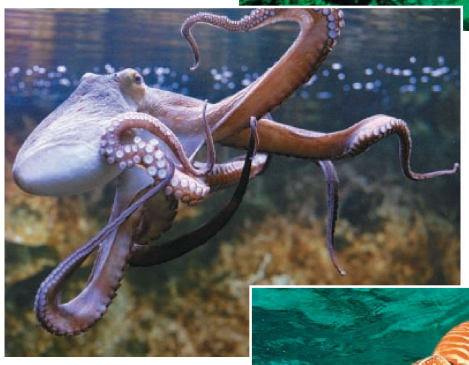
Cephalopods are active marine predators **(Figure 33.20)**. They use their tentacles to grasp prey, which they then bite with beak-like jaws and immobilize with a poison present in their saliva. The foot of a cephalopod has become modified into a muscular excurrent siphon and part of the tentacles. Squids dart about by drawing water into their mantle cavity and then firing a jet of water through the excurrent siphon; they steer by pointing the siphon in different directions. Octopuses use a similar mechanism to escape predators.

The mantle covers the visceral mass of cephalopods, but the shell is generally reduced and internal (in most species) or missing altogether (in some cuttlefishes and some octopuses).

▼ Figure 33.20 Cephalopods.

▶ Squids are speedy carnivores with beak-like jaws and well-developed eyes.





◀ Octopuses are considered among the most intelligent invertebrates.



▶ Chambered nautiluses are the only living cephalopods with an external shell.

One small group of cephalopods with external shells, the chambered nautiluses, survives today.

Cephalopods are the only molluscs with a *closed circulatory system*, in which the blood remains separate from fluid in the body cavity. They also have well-developed sense organs and a complex brain. The ability to learn and behave in a complex manner is probably more critical to fast-moving predators than to sedentary animals such as clams.

The ancestors of octopuses and squids were probably shelled molluscs that took up a predatory lifestyle; the shell was lost in later evolution. Shelled cephalopods called **ammonites**, some of them as large as truck tires, were the dominant invertebrate predators of the seas for hundreds of millions of years until their disappearance during the mass extinction at the end of the Cretaceous period, 66 million years ago.

Most species of squid are less than 75 cm long, but some are much larger. The giant squid (*Architeuthis dux*), for example, has an estimated maximum length of 13 m for females and 10 m for males. The colossal squid (*Mesonychoteuthis hamiltoni*), is even larger, with an estimated maximum length of 14 m. Unlike *A. dux*, which has large suckers and small teeth on its tentacles, *M. hamiltoni* has two rows of sharp hooks at the ends of its tentacles that can inflict deadly lacerations.

It is likely that *A. dux* and *M. hamiltoni* spend most of their time in the deep ocean, where they may feed on large fishes. Remains of both giant squid species have been found in the stomachs of sperm whales, which are probably their only natural predator. Scientists first photographed *A. dux* in the wild in 2005 while it was attacking baited hooks at a depth of 900 m. *M. hamiltoni* has yet to be observed in nature. Overall, much remains to be learned about these marine giants.

Protecting Freshwater and Terrestrial Molluscs

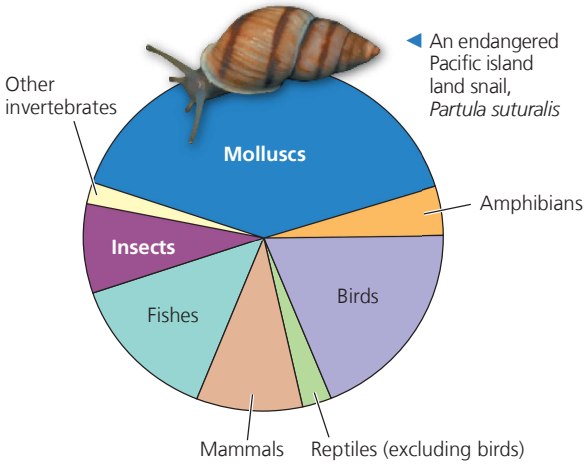
Species extinction rates have increased dramatically in the last 400 years, raising concern that a sixth, human-caused mass extinction may be under way (see Concept 25.4). Among the many taxa under threat, molluscs have the dubious distinction of being the animal group with the largest number of documented extinctions **(Figure 33.21)**.

Threats to molluscs are especially severe in two groups: freshwater bivalves and terrestrial gastropods. For example, the pearl mussels, a group of freshwater bivalves that can make natural pearls (gems that form when a mussel or oyster secretes layers of a lustrous coating around a grain of sand or other small irritant), are among the world's most endangered animals. Roughly 10% of the 300 pearl mussel species that once lived in North America have become extinct in the last 100 years, and over two-thirds of those that remain are threatened by extinction. Terrestrial gastropods, such as the snail in Figure 33.21, are faring no better. Hundreds of Pacific island land snails have disappeared since 1800. Overall, more than 50% of the Pacific island land snails are extinct or under imminent threat of extinction.

Threats faced by freshwater and terrestrial molluscs include habitat loss, pollution, competition or predation by non-native species, and overharvesting by humans. Is it too late to protect these molluscs? In some locations, reducing water pollution and changing how water is released from dams have led to dramatic rebounds in pearl mussel populations. Such results provide hope that with corrective measures, other endangered mollusc species can be revived.

▼ Figure 33.21 The silent extinction. Molluscs account for a largely unheralded but sobering 40% of all documented extinctions of animal species. These extinctions have resulted from human actions such as habitat loss and overharvesting. Many pearl mussel populations, for example, were driven to extinction by overharvesting for their shells, which were used to make buttons and other goods. Land snails are highly vulnerable to the same threats; like pearl mussels, they are among the world's most imperiled animal groups.

MAKE CONNECTIONS *Freshwater bivalves feed on and can reduce the abundance of photosynthetic protists and bacteria. As such, what types of effects would the extinction of freshwater bivalves likely have on aquatic communities (see Concept 28.6)?*



▲ Recorded extinctions of animal species



▲ Workers on a mound of pearl mussels killed to make buttons (ca. 1919)

Annelids

Annelida means "little rings," referring to the annelid body's resemblance to a series of fused rings. Annelids are segmented worms that live in the sea, in most freshwater habitats, and in damp soil. Annelids, which have a coelom (and no hemocoel), range in length from less than 1 mm to more than 3 m.

Traditionally, the phylum Annelida was divided into three main groups, Polychaeta (the polychaetes), Oligochaeta (the oligochaetes), and Hirudinea (the leeches). The names of the first two of these groups reflected the relative number of chaetae, bristles made of chitin, on their bodies: polychaetes (from the Greek *poly*, many, and *chaitē*, long hair) have many more chaetae per segment than do oligochaetes.

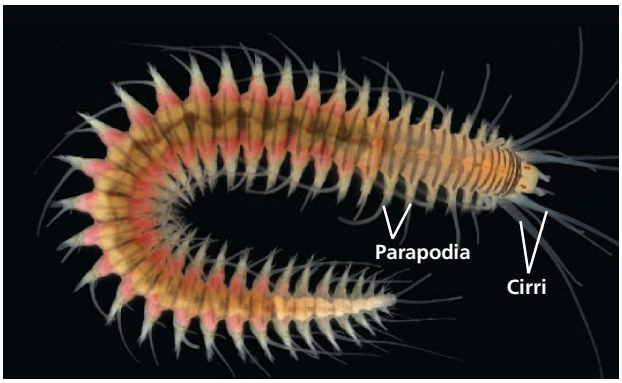
However, a 2011 phylogenomic study and other recent molecular analyses have indicated that the oligochaetes are a subgroup of the polychaetes, making the polychaetes (as defined morphologically) a paraphyletic group. Likewise, the leeches have been shown to be a subgroup of the oligochaetes. As a result, these traditional names are no longer used to describe the evolutionary history of the annelids. Instead, current evidence indicates that the annelids can be divided into two major clades, Errantia and Sedentaria—a grouping that reflects broad differences in lifestyle.

Errantians

Clade Errantia (from the Old French *errant*, traveling) is a large and diverse group, most of whose members are marine **(Figure 33.22)**. As their name suggests, many errantians are mobile; some swim among the plankton (small, drifting organisms), while many others crawl on or burrow in the seafloor. Many are predators, while others are grazers that feed on large, multicellular algae. The group also includes some relatively immobile species, such as the tube-dwelling *Platynereis*, a marine species that recently has become a model organism for studying neurobiology and development.

In many errantians, each body segment has a pair of prominent paddle-like or ridge-like structures called parapodia ("beside feet") that function in locomotion (see Figure 33.22).

▼ Figure 33.22 An errantian, the predator *Nereimyra punctata*. This marine annelid ambushes prey from burrows it has constructed on the seafloor. *N. punctata* hunts by touch, detecting its prey with long sensory organs called cirri that extend from the burrow.



Each parapodium has numerous chaetae. (Possession of parapodia with numerous chaetae is not unique to Errantia, however, as some members of the other major clade of annelids, Sedentaria, also have these features.) In many species, the parapodia are richly supplied with blood vessels and also function as gills. Errantians also tend to have well-developed jaws and sensory organs, as might be expected of predators or grazers that move about in search of food.

Sedentarians

Species in the other major clade of annelids, Sedentaria (from the Latin *sedere*, sit), tend to be less mobile than those in Errantia. Some species burrow slowly through marine sediments or soil, while others live within tubes that protect and support their soft bodies. Tube-dwelling sedentarians often have elaborate gills or tentacles used for filter feeding **(Figure 33.23)**.

Although the Christmas tree worm shown in Figure 33.23 once was classified as a "polychaete," current evidence indicates it is a sedentarian. The clade Sedentaria also contains former "oligochaetes," including the two groups we turn to next, the leeches and the earthworms.

Leeches Some leeches are parasites that suck blood by attaching temporarily to other animals, including humans **(Figure 33.24)**, but most are predators that feed on other

▼ Figure 33.23 The Christmas tree worm, *Spirobranchus giganteus*. This sedentarian's two tree-shaped whorls are tentacles, which it uses in gas exchange and to collect food particles from the water. The tentacles emerge from a calcium carbonate tube secreted by the worm that protects and supports its soft body.



▶ Figure 33.24 A leech. A nurse applied this medicinal leech (*Hirudo medicinalis*) to a patient's sore thumb to drain blood from a hematoma (an abnormal accumulation of blood around an internal injury).

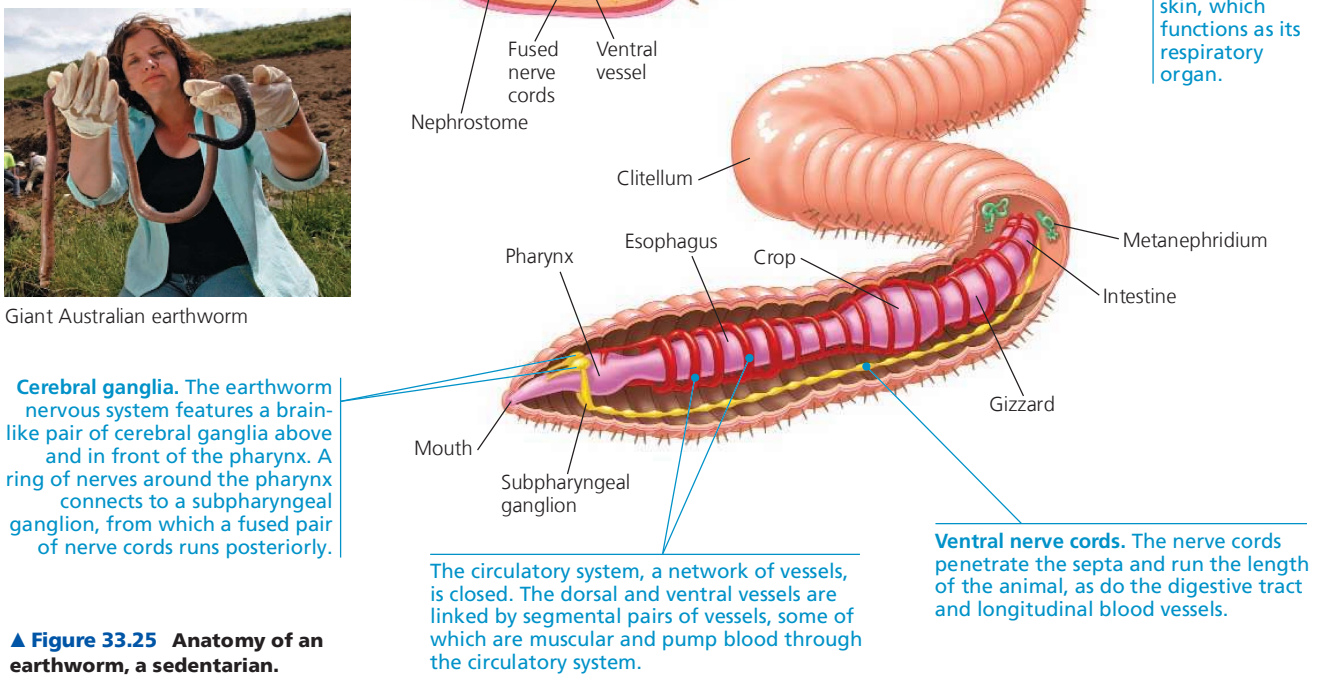


invertebrates. Leeches range in length from 1 to 30 cm. Most leeches inhabit fresh water, but there are also marine species and terrestrial leeches, which live in moist vegetation. Some parasitic species use bladelike jaws to slit the skin of their host. The host is usually oblivious to this attack because the leech secretes an anesthetic. After making the incision, the leech secretes a chemical, hirudin, which keeps the blood of the host from coagulating near the incision. The parasite then sucks as much blood as it can hold, often more than ten times its own weight. After this gorging, a leech can last for months without another meal.

Until the 20th century, leeches were frequently used for bloodletting. Today they are used to drain blood that accumulates in tissues following certain injuries or surgeries. In addition, forms of hirudin produced with recombinant DNA techniques can be used to dissolve unwanted blood clots that form during surgery or as a result of heart disease.

Earthworms Earthworms eat their way through the soil, extracting nutrients as the soil passes through the alimentary canal. Undigested material, mixed with mucus secreted into the canal, is eliminated as fecal castings through the anus. Farmers value earthworms because the animals till and aerate the earth, and their castings improve the texture of the soil. (Charles Darwin estimated that one acre of farmland contains about 50,000 earthworms, producing 18 tons of castings per year.)

A guided tour of the anatomy of an earthworm, which is representative of annelids, is shown in **Figure 33.25**.



Giant Australian earthworm

▲ Figure 33.25 Anatomy of an earthworm, a sedentarian.

Earthworms are hermaphrodites, but they do cross-fertilize. Two earthworms mate by aligning themselves in opposite directions in such a way that they exchange sperm, and then they separate. Some earthworms can also reproduce asexually by fragmentation followed by regeneration.

As a group, Lophotrochozoa encompasses a remarkable range of body plans, as illustrated by members of such phyla as Syndermata, Ectoprocta, Mollusca, and Annelida. Next we'll explore the diversity of Ecdysozoa, a dominant presence on Earth in terms of sheer number of species.

CONCEPT CHECK 33.3

1. Explain how tapeworms can survive without a body cavity, a mouth, a digestive system, or an excretory system.
2. Annelid anatomy can be described as "a tube within a tube." Explain.
3. **MAKE CONNECTIONS** Explain how the molluscan foot in gastropods and the excurrent siphon in cephalopods represent examples of descent with modification (see Concept 22.2).

For suggested answers, see Appendix A.

CONCEPT 33.4

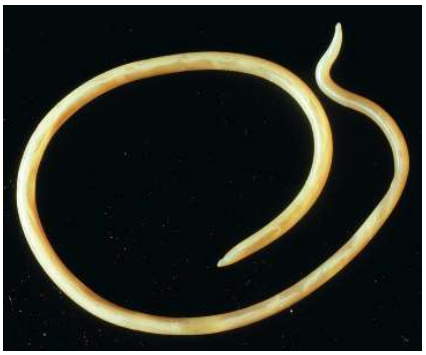
Ecdysozoans are the most species-rich animal group



Although defined primarily by molecular evidence, the clade Ecdysozoa includes animals that shed a **cuticle** (a tough external coat) as they grow. In fact, the group derives its name from this process, which is called *ecdysis*, or **molting**. Ecdysozoa includes about eight animal phyla and contains more known species than all other animal, protist, fungus, and plant groups combined. Here we'll focus on the two largest ecdysozoan phyla, the nematodes and arthropods, which are among the most successful and abundant of all animal groups.

Nematodes

Among the most ubiquitous of animals, nematodes (phylum Nematoda), or roundworms, are found in most aquatic habitats, in the soil, in the moist tissues of plants, and in the body fluids and tissues of animals. The cylindrical bodies of nematodes range from less than 1 mm to more than 1 m long, often tapering to a fine tip at the posterior end and to a blunter tip at the anterior end **(Figure 33.26)**. A nematode's body is covered by a tough cuticle (a type of exoskeleton); as the worm grows, it periodically sheds its old cuticle and secretes a new, larger one. Nematodes have an alimentary canal, though they lack a circulatory system. Nutrients are transported throughout the body via fluid in the hemocoel. The body wall muscles are all longitudinal, and their contraction produces a thrashing motion.

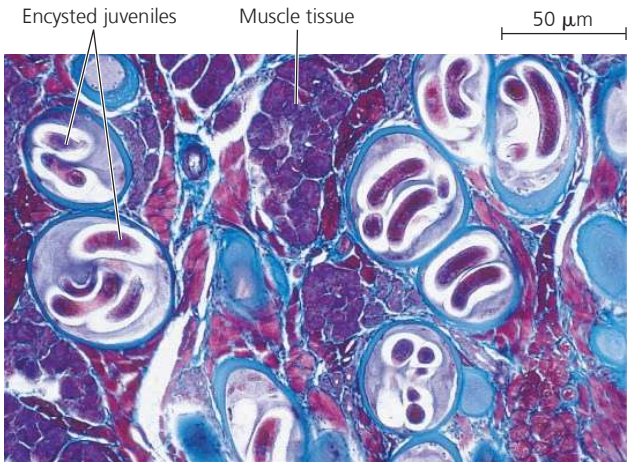


▶ Figure 33.26 A free-living nematode. (colorized SEM)

Multitudes of nematodes live in moist soil and in decomposing organic matter on the bottoms of lakes and oceans. While 25,000 species are known, perhaps 20 times that number actually exist. These free-living worms play an important role in decomposition and nutrient cycling, but little is known about most species. One species of soil nematode, *Caenorhabditis elegans*, however, is very well studied and has become a model research organism in biology (see Concept 47.3). Ongoing studies of *C. elegans* are providing insight into mechanisms involved in aging in humans, as well as many other topics.

Phylum Nematoda includes many species that parasitize plants, and some are major agricultural pests that attack the roots of crops. Other nematodes parasitize animals. Some of these species benefit humans by attacking insects such as cutworms that feed on the roots of crop plants. On the other hand, humans are hosts to at least 50 nematode species, including various pinworms and hookworms. One notorious nematode is *Trichinella spiralis*, the worm that causes trichinosis **(Figure 33.27)**. Humans acquire this nematode by eating raw or undercooked pork or other meat (including wild game such as bear or walrus) that has juvenile worms encysted in the muscle tissue. Within the human intestines, the juveniles develop into sexually mature adults. Females

▼ Figure 33.27 Juveniles of the parasitic nematode *Trichinella spiralis* encysted in human muscle tissue. (LM)



burrow into the intestinal muscles and produce more juveniles, which bore through the body or travel in lymphatic vessels to other organs, including skeletal muscles, where they encyst.

Parasitic nematodes have an extraordinary molecular toolkit that enables them to redirect some of the cellular functions of their hosts. Some species inject their plant hosts with molecules that induce the development of root cells, which then supply nutrients to the parasites. When *Trichinella* parasitizes animals, it regulates the expression of specific muscle cell genes encoding proteins that make the cell elastic enough to house the nematode. Additionally, the infected muscle cell releases signals that promote the growth of new blood vessels, which then supply the nematode with nutrients.

Arthropods

Zoologists estimate that there are about a billion billion (10^{18}) arthropods living on Earth. More than 1 million arthropod species have been described, most of which are insects. In fact, two out of every three known species are arthropods, and members of the phylum Arthropoda can be found in nearly all habitats of the biosphere. By the criteria of species diversity, distribution, and sheer numbers, arthropods must be regarded as the most successful of all animal phyla.

Arthropod Origins

Biologists hypothesize that the diversity and success of **arthropods** are related to their body plan—their segmented body, hard exoskeleton, and jointed appendages. How did this body plan arise and what advantages did it provide?

The earliest fossils of arthropods are from the Cambrian explosion (535–525 million years ago), indicating that the arthropods are at least that old. The fossil record of the Cambrian explosion also contains many species of *lobopods*, a group from which arthropods may have evolved. Lobopods such as *Hallucigenia* (see Figure 32.7) had segmented bodies, but most of their body segments were identical to one another. Early arthropods, such as the trilobites, also showed little variation from segment to segment **(Figure 33.28)**. As arthropods continued to evolve, groups of segments tended to become functionally united into "body regions" specialized for tasks such as feeding, walking, or swimming. These evolutionary changes resulted not only in great diversification but also in efficient body plans that permit the division of labor among different body regions.

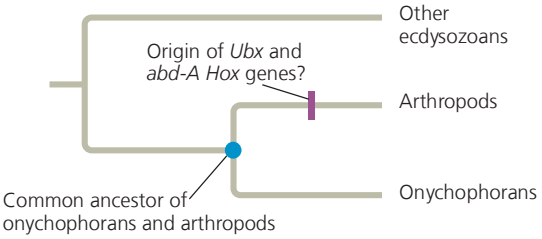


▶ Figure 33.28 A trilobite fossil. Trilobites were common denizens of the shallow seas throughout the Paleozoic era but disappeared with the great Permian extinctions about 250 million years ago. Paleontologists have described about 4,000 trilobite species.

▼ Figure 33.29 Inquiry

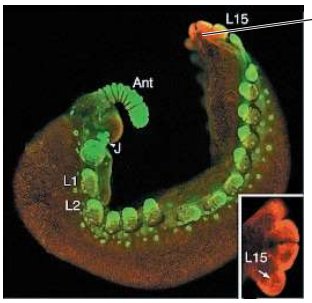
Did the arthropod body plan result from new *Hox* genes?

Experiment One hypothesis suggests that the arthropod body plan resulted from the origin (by gene duplication and subsequent mutations) of two unusual *Hox* genes found in arthropods: *Ultrabithorax* (*Ubx*) and *abdominal-A* (*abd-A*). Researchers tested this hypothesis using onychophorans, a group of invertebrates closely related to arthropods. Unlike many living arthropods, onychophorans have a body plan in which most body segments are identical to one another. If the origin of the *Ubx* and *abd-A Hox* genes drove the evolution of body segment diversity in arthropods, these genes probably arose on the arthropod branch of the evolutionary tree:



According to this hypothesis, *Ubx* and *abd-A* would not have been present in the common ancestor of arthropods and onychophorans; hence, onychophorans should not have these genes. The researchers examined the *Hox* genes of the onychophoran *Acanthokara kaputensis.*

Results The onychophoran *A. kaputensis* has all arthropod *Hox* genes, including *Ubx* and *abd-A*.



Red indicates the body regions of this onychophoran embryo in which *Ubx* or *abd-A* genes were expressed. (The inset shows this area enlarged.)

Ant = antenna
J = jaws
L1–L15 = body segments

Conclusion The evolution of increased body segment diversity in arthropods was not related to the origin of new *Hox* genes.

Data from J. K. Grenier et al., Evolution of the entire arthropod *Hox* gene set predated the origin and radiation of the onychophoran/arthropod clade, *Current Biology* 7:547–553 (1997).

WHAT IF? *Suppose* A. kaputensis *did not have the* Ubx *and* abd-A Hox *genes. How would the conclusions of this study have been affected? Explain.*

What genetic changes led to the increasing complexity of the arthropod body plan? Arthropods today have two unusual *Hox* genes, both of which influence segmentation. To test whether these genes could have driven the evolution of increased body segment diversity in arthropods, researchers studied *Hox* genes in onychophorans (see Figure 33.2), close relatives of arthropods **(Figure 33.29)**. Their results indicate that the diversity of arthropod body plans did *not* arise from the acquisition of new *Hox* genes. Instead, the evolution of body segment diversity in arthropods was probably driven by changes in the sequence or regulation of existing *Hox* genes (see Concept 25.5).

General Characteristics of Arthropods

Over the course of evolution, the appendages of some arthropods have become modified, specializing in functions such as walking, feeding, sensory reception, reproduction, and defense. Like the appendages from which they were derived, these modified structures are jointed and come in pairs. **Figure 33.30** illustrates the diverse appendages and other arthropod characteristics of a lobster.

The body of an arthropod is completely covered by the cuticle, an exoskeleton constructed from layers of protein and the polysaccharide chitin. As you know if you've ever eaten a crab or lobster, the cuticle can be thick and hard over some parts of the body and thin and flexible over others, such as the joints. The rigid exoskeleton protects the animal and provides points of attachment for the muscles that move the appendages. But it also prevents the arthropod from growing, unless it occasionally sheds its exoskeleton and produces a larger one. This molting process is energetically expensive, and it leaves the arthropod vulnerable to predation and other dangers until its new, soft exoskeleton hardens.

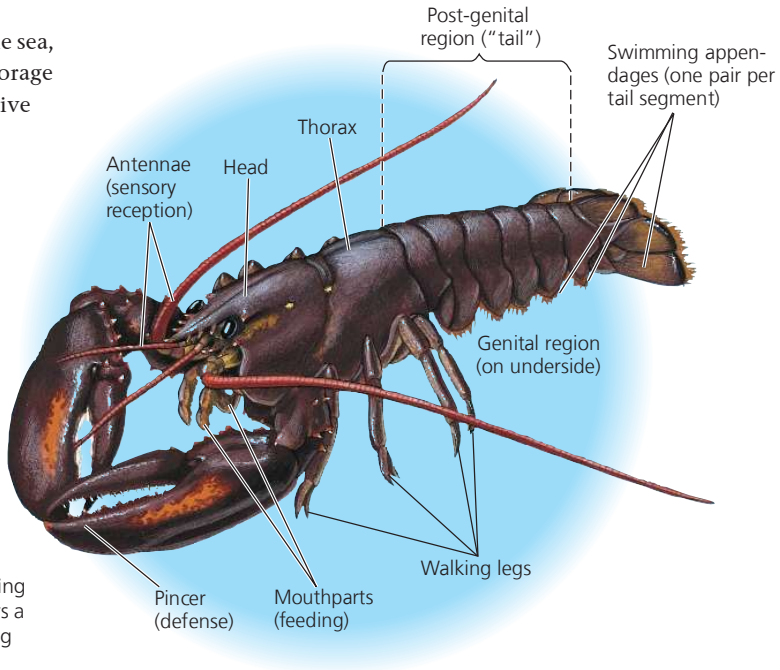
When the arthropod exoskeleton first evolved in the sea, its main functions were probably protection and anchorage for muscles, but it later enabled certain arthropods to live on land. The exoskeleton's relative impermeability to water helped prevent desiccation, and its strength provided support when arthropods left the buoyancy of water. Fossil evidence suggests that arthropods were among the first animals to colonize land, roughly 450 million years ago. These fossils include fragments of arthropod remains, as well as possible millipede burrows. Arthropod fossils from several continents indicate that by 410 million years ago, millipedes, centipedes, spiders, and a variety of wingless insects all had colonized land.

Arthropods have well-developed sensory organs, including eyes, olfactory (smell) receptors, and antennae that function in both touch and smell. Most sensory organs are concentrated at the anterior end of the animal, although there are interesting exceptions. Female butterflies, for example, "taste" plants using sensory organs on their feet.

Like many molluscs, arthropods have an **open circulatory system**, in which fluid called *hemolymph* is propelled by a heart through short arteries and then into the hemocoel—the body cavity surrounding the tissues and organs. (The term *blood* is generally reserved for fluid in a closed circulatory system.) Hemolymph reenters the arthropod heart through pores that are usually equipped with valves. In most arthropods, the coelom that forms in the embryo becomes much reduced as development progresses, and the hemocoel becomes the main body cavity in adults.

A variety of specialized gas exchange organs have evolved in arthropods. These organs allow the diffusion of respiratory gases in spite of the exoskeleton. Most aquatic species have gills with thin, feathery extensions that expose a large surface area to the surrounding water. Terrestrial arthropods generally have internal surfaces specialized for gas exchange. For example, most insects have tracheal systems, branched air ducts leading into the interior of the body from pores in the cuticle.

Morphological and molecular data suggest that living arthropods consist of three major lineages that diverged early in the phylum's evolution: **chelicerates** (sea spiders, horseshoe crabs, scorpions, ticks, mites, and spiders); **myriapods**



▶ Figure 33.30 External anatomy of an arthropod. Many of the distinctive features of arthropods are apparent in this dorsal view of a lobster. The body is segmented, but this character is obvious only in the post-genital region or "tail," located behind the genitals. The appendages (including antennae, pincers, mouthparts, walking legs, and swimming appendages) are jointed. The head bears a pair of compound (multilens) eyes. The whole body, including appendages, is covered by an exoskeleton.

(centipedes and millipedes); and **pancrustaceans** (a recently defined, diverse group that includes insects as well as lobsters, shrimp, barnacles, and other crustaceans).

Chelicerates

Chelicerates (clade Chelicerata) are named for clawlike feeding appendages called **chelicerae**, which serve as pincers or fangs. Chelicerates lack antennae, and most have simple eyes (eyes with a single lens).

The earliest chelicerates were **eurypterids**, or water scorpions. These marine and freshwater predators grew up to 3 m long; it is thought that some species could have walked on land, much as land crabs do today. Most of the marine chelicerates, including all of the eurypterids, are extinct. Among the marine chelicerates that survive today are the sea spiders (pycnogonids) and horseshoe crabs **(Figure 33.31)**.

The bulk of modern chelicerates are **arachnids**, a group that includes scorpions, spiders, ticks, and mites **(Figure 33.32)**. Nearly all ticks are bloodsucking parasites that live on the body surfaces of reptiles or mammals. Parasitic mites live on or in a wide variety of vertebrates, invertebrates, and plants.

Arachnids have six pairs of appendages: the chelicerae; a pair of appendages called *pedipalps* that function in sensing, feeding, defense, or reproduction; and four pairs of walking legs. Spiders use their fang-like chelicerae, which are equipped with poison glands, to attack prey. As the chelicerae pierce the prey, the spider secretes digestive juices onto the prey's torn tissues. The food softens, and the spider sucks up the liquid meal. In most spiders, gas exchange is carried out by **book lungs**, stacked platelike structures contained in an internal chamber **(Figure 33.33)**. The extensive surface area of these respiratory organs enhances the exchange of O_2 and CO_2 between the hemolymph and air.

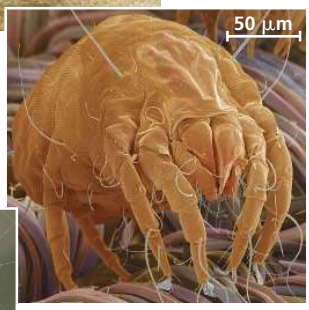
A unique adaptation of many spiders is the ability to catch insects by constructing webs of silk, a liquid protein produced by specialized abdominal glands. The silk is spun by organs called spinnerets into fibers that then solidify. Each spider engineers a web characteristic of its species and builds it perfectly on the first try, indicating that this complex behavior is inherited. Various spiders also use silk in other ways: as droplines for rapid escape, as a cover for eggs, and even as "gift wrap" for food that males offer females during courtship. Many small spiders also extrude silk into the air and let themselves be transported by wind, a behavior known as "ballooning."

▼ Figure 33.31 Horseshoe crabs (*Limulus polyphemus*). Common on the Atlantic and Gulf coasts of the United States, these "living fossils" have changed little in hundreds of millions of years. They are surviving members of a rich diversity of chelicerates that once filled the seas.

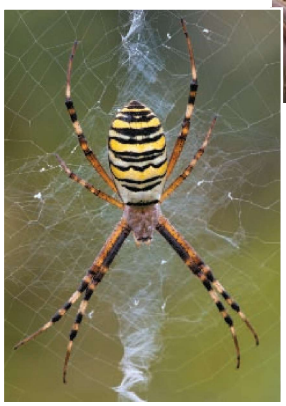




▲ Scorpions have pedipalps that are pincers specialized for defense and the capture of food. The tip of the tail bears a poisonous stinger.



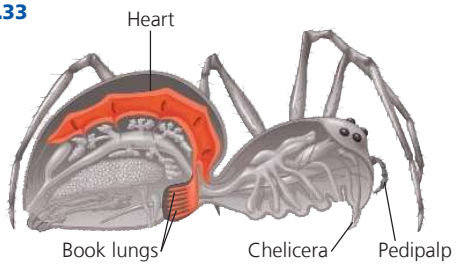
▲ Dust mites are ubiquitous scavengers in human dwellings but are harmless except to those people who are allergic to them (colorized SEM).



◀ Web-building spiders are generally most active during the daytime.

▲ Figure 33.32 Arachnids.

▶ Figure 33.33 Book lungs.



Myriapods

Millipedes and centipedes belong to the clade Myriapoda **(Figure 33.34)**. All living myriapods are terrestrial. The myriapod head has a pair of antennae and three pairs of



(a) Millipede

(b) Centipede

▲ **Figure 33.34** **Myriapods.**

appendages modified as mouthparts, including the jaw-like mandibles.

Millipedes have a large number of legs, though fewer than the thousand their name implies. Each trunk segment is formed from two fused segments and bears two pairs of legs (see Figure 33.34a). Millipedes eat decaying leaves and other plant matter. They may have been among the earliest animals on land, living on mosses and early vascular plants.

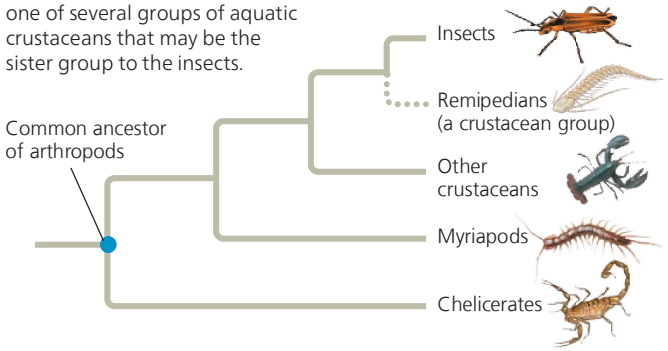
Unlike millipedes, centipedes are carnivores. Each segment of a centipede's trunk region has one pair of legs (see Figure 33.34b). Centipedes have poison claws on their foremost trunk segment that paralyze prey and aid in defense.

Pancrustaceans

A series of recent papers present evidence that terrestrial insects are more closely related to lobsters and other crustaceans than they are to the terrestrial group we just discussed, the myriapods (millipedes and centipedes). These studies also suggest that the diverse group of organisms referred to as crustaceans are paraphyletic: Some lineages of crustaceans are more closely related to insects than they are to other crustaceans **(Figure 33.35)**. However, together the insects and crustaceans form a clade, which systematists have named Pancrustacea (from the Greek *pan*, all). We turn next to a description of the members of Pancrustacea, focusing first on crustaceans and then on the insects.

Crustaceans Crustaceans (crabs, lobsters, shrimps, barnacles, and many others) thrive in a broad range of marine, freshwater, and terrestrial environments. Many crustaceans have highly specialized appendages. Lobsters and crayfishes, for instance, have a toolkit of 19 pairs of appendages (see Figure 33.30). The anterior-most appendages form two pairs of antennae; crustaceans are the only arthropods with two pairs. Three or more pairs of appendages are modified as mouthparts, including the hard mandibles. Walking legs are present on the thorax, and, unlike their terrestrial relatives, the insects, crustaceans also have appendages on their postgenital region, or "tail."

▼ **Figure 33.35** **The phylogenetic position of the insects.** Recent results have shown that the insects are nested within lineages of aquatic crustaceans. The remipedians are one of several groups of aquatic crustaceans that may be the sister group to the insects.



DRAW IT *Circle the portions of this tree that comprise the clade Pancrustacea.*

Small crustaceans exchange gases across thin areas of the cuticle; larger species have gills. Nitrogenous wastes also diffuse through thin areas of the cuticle, but a pair of glands regulates the salt balance of the hemolymph.

Sexes are separate in most crustaceans. In the case of lobsters and crayfishes, the male uses a specialized pair of abdominal appendages to transfer sperm to the reproductive pore of the female during copulation. Most aquatic crustaceans go through one or more swimming larval stages.

One of the largest groups of crustaceans (numbering over 11,000 species) is the *isopods*, which include terrestrial, freshwater, and marine species. Some isopod species are abundant in habitats at the bottom of the deep ocean. Among the terrestrial isopods are the pill bugs, or wood lice, common on the undersides of moist logs and leaves.

Lobsters, crayfishes, crabs, and shrimps are all relatively large crustaceans called *decapods* **(Figure 33.36)**. The cuticle of decapods is hardened by calcium carbonate. Most decapod species are marine. Crayfishes, however, live in fresh water, and some tropical crabs live on land.

▼ **Figure 33.36** **A ghost crab, an example of a decapod.** Ghost crabs live on sandy ocean beaches worldwide. Primarily nocturnal, they take shelter in burrows during the day.





▲ **Figure 33.37** **Krill.** These planktonic crustaceans are consumed in vast quantities by some whales.



▲ **Figure 33.38** **Barnacles.** The jointed appendages projecting from the barnacles' shells capture organisms and organic particles suspended in the water.

Many small crustaceans are important members of marine and freshwater plankton communities. Planktonic crustaceans include many species of *copepods*, which are among the most numerous of all animals. Some copepods are grazers that feed upon algae, while others are predators that eat small animals (including smaller copepods!). Copepods are rivaled in abundance by the shrimplike krill, which grow to about 5 cm long **(Figure 33.37)**. A major food source for baleen whales (including blue whales, humpbacks, and right whales), krill are now being harvested in great numbers by humans for food and agricultural fertilizer. The larvae of many larger-bodied crustaceans are also planktonic.

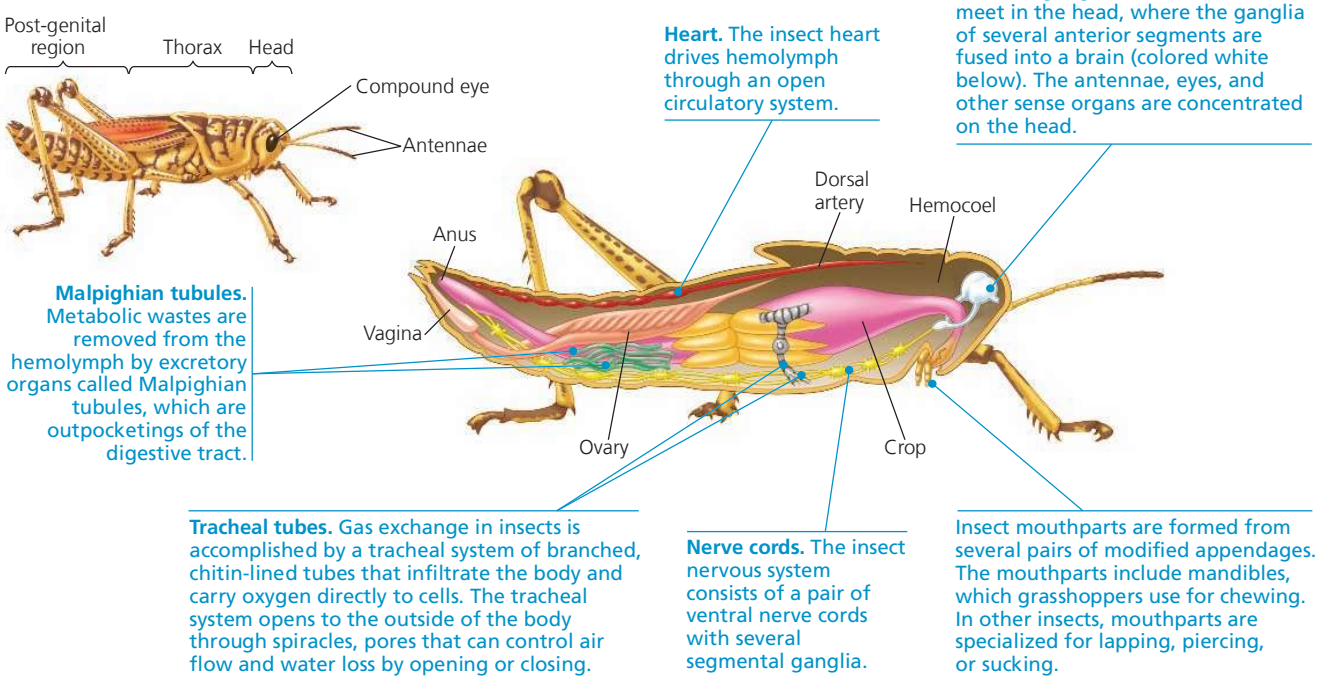
With the exception of a few parasitic species, barnacles are a group of sessile crustaceans whose cuticle is hardened into a shell containing calcium carbonate **(Figure 33.38)**. Most barnacles anchor themselves to rocks, boat hulls, pilings, and other submerged surfaces. Their natural adhesive is as strong as synthetic glues. These barnacles feed by extending appendages from their shell to strain food from the water. Barnacles were not recognized as crustaceans until the 1800s, when naturalists discovered that barnacle larvae resemble the larvae of other crustaceans. The remarkable mix of unique traits and crustacean homologies found in barnacles was a major inspiration to Charles Darwin as he developed his theory of evolution.

We turn now to a group nested within the paraphyletic crustaceans, the insects.

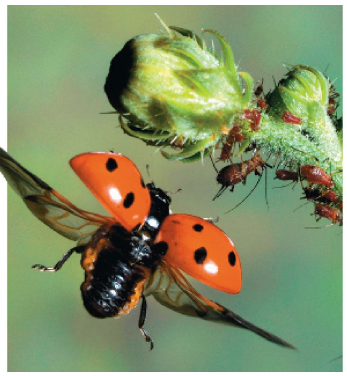
Insects Insects and their six-legged terrestrial relatives form an enormous clade, Hexapoda; we'll focus here on the insects, since as a group they have more described species than all other eukaryotic groups combined. Insects live in almost every terrestrial habitat and in fresh water, and flying insects fill the air. Insects are rare, though not absent, in marine habitats. The internal anatomy of an insect includes several complex organ systems, which are highlighted in **Figure 33.39**.

The oldest insect fossils date to about 415 million years ago. Later, an explosion in insect diversity took place when insect flight evolved during the Carboniferous and Permian periods (359–252 million years ago). An animal that can fly can escape predators, find food and mates, and disperse to new habitats more effectively than an animal that must crawl about on the

▼ **Figure 33.39** **Anatomy of a grasshopper, an insect.** The insect body has three regions: head, thorax, and post-genital region. The segmentation of the thorax and post-genital region is obvious, but the segments that form the head are fused.



ground. Many insects have one or two pairs of wings that emerge from the dorsal side of the thorax. Because the wings are extensions of the cuticle, insects can fly without sacrificing any walking legs **(Figure 33.40)**. By contrast, the flying vertebrates—birds and bats—have one of their two pairs of walking legs modified into wings, making some of these species clumsy on the ground.



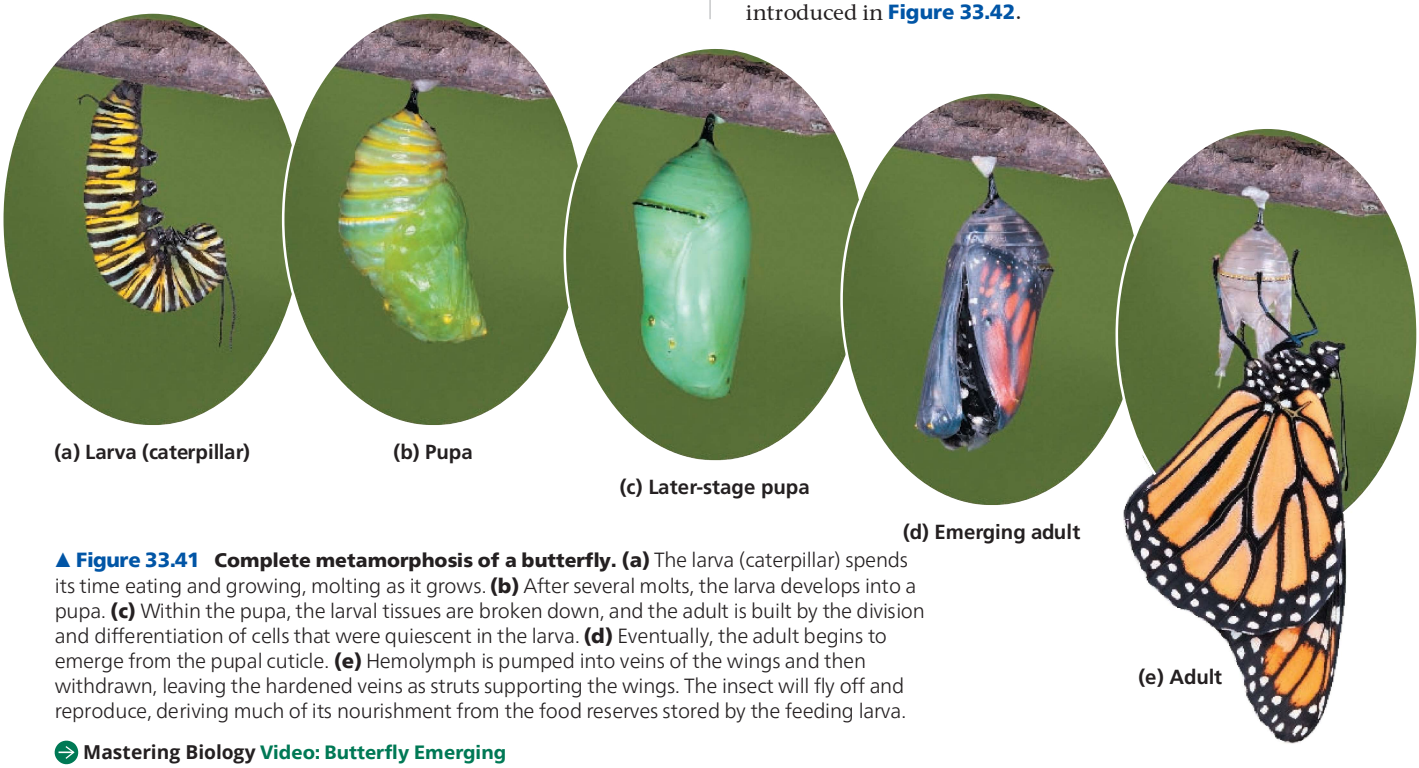
▲ Figure 33.40 Ladybird beetle in flight.

Insects also radiated in response to the origin of new plant species, which provided new sources of food. By the speciation mechanisms described in Concept 24.2, an insect population feeding on a new plant species can diverge from other populations, eventually forming a new species of insect. A fossil record of diverse insect mouthparts, for example, suggests that specialized modes of feeding on gymnosperms and other Carboniferous plants contributed to early adaptive radiations of insects. Later, a major increase in insect diversity appears to have been stimulated by the evolutionary expansion of flowering plants during the mid-Cretaceous period (about 100 million years ago). Although insect and plant diversity decreased during the Cretaceous mass extinction, both groups have rebounded over the past 66 million years. Increases in the diversity of particular insect groups have often been associated with radiations of the flowering plants on which they fed.

Many insects undergo metamorphosis during their development. In the **incomplete metamorphosis** of grasshoppers and some other insect groups, the young (called nymphs) resemble adults but are smaller, have different body proportions, and lack wings. The nymph undergoes a series of molts, each time looking more like an adult. With the final molt, the insect reaches full size, acquires wings, and becomes sexually mature. Insects with **complete metamorphosis** have larval stages specialized for eating and growing that are known by such names as caterpillar, maggot, or grub. The larval stage looks entirely different from the adult stage, which is specialized for dispersal and reproduction. Metamorphosis from the larval stage to the adult occurs during a pupal stage **(Figure 33.41)**.

Reproduction in insects is usually sexual, with separate male and female individuals. Adults come together and recognize each other as members of the same species by advertising with bright colors (as in butterflies), sounds (as in crickets), or odors (as in moths). Fertilization is generally internal. In most species, sperm are deposited directly into the female's vagina at the time of copulation, though in some species the male deposits a sperm packet outside the female, and the female picks it up. An internal structure in the female called the spermatheca stores the sperm, usually enough to fertilize more than one batch of eggs. Many insects mate only once in a lifetime. After mating, a female often lays her eggs on an appropriate food source where the next generation can begin eating as soon as it hatches.

Insects are classified in more than 30 orders, 8 of which are introduced in **Figure 33.42**.



▲ Figure 33.41 Complete metamorphosis of a butterfly. (a) The larva (caterpillar) spends its time eating and growing, molting as it grows. **(b)** After several molts, the larva develops into a pupa. **(c)** Within the pupa, the larval tissues are broken down, and the adult is built by the division and differentiation of cells that were quiescent in the larva. **(d)** Eventually, the adult begins to emerge from the pupal cuticle. **(e)** Hemolymph is pumped into veins of the wings and then withdrawn, leaving the hardened veins as struts supporting the wings. The insect will fly off and reproduce, deriving much of its nourishment from the food reserves stored by the feeding larva.

Mastering Biology Video: Butterfly Emerging

▼ Figure 33.42 Exploring Insect Diversity

Although there are more than 30 orders of insects, we'll focus on just 8 here. Two orders of wingless insects, the bristletails (Archaeognatha) and silverfish (Zygentoma), diverged from other insects early in insect evolution. Evolutionary relationships among the other groups discussed here are under debate and so are not depicted on the tree.



Archaeognatha (bristletails; 350 species)

These wingless insects are found under bark and in other moist, dark habitats such as leaf litter, compost piles, and rock crevices. They feed on algae, plant debris, and lichens.



Zygentoma (silverfish; 450 species)

These small, wingless insects have a flattened body and reduced eyes. They live in leaf litter or under bark. They can also infest buildings, where they can become pests.

Winged insects (many orders; six are shown below)

Complete metamorphosis



Coleoptera (beetles; 350,000 species)

Beetles, such as this weevil in the genus *Rhinastus*, constitute the most species-rich order of insects. They have two pairs of wings, one of which is thick and stiff, the other membranous. They have an armored exoskeleton and mouthparts adapted for biting and chewing.



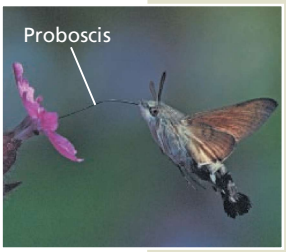
Diptera (151,000 species)

Dipterans have one pair of wings; the second pair has become modified into balancing organs called halteres. Their mouthparts are adapted for sucking, piercing, or lapping. Flies and mosquitoes are among the best-known dipterans, which live as scavengers, predators, and parasites. Like many other insects, flies such as this red tachinid (*Adejeania vexatrix*) have well-developed compound eyes that provide a wide-angle view and excel at detecting fast movements.



Hymenoptera (125,000 species)

Most hymenopterans, which include ants, bees, and wasps, are highly social insects. They have two pairs of membranous wings, a mobile head, and chewing or sucking mouthparts. The females of many species have a posterior stinging organ. Many species, such as this European paper wasp (*Polistes dominulus*), build elaborate nests.



Lepidoptera (120,000 species)

Butterflies and moths have two pairs of wings covered with tiny scales. To feed, they uncoil a long proboscis, visible in this photograph of a hummingbird hawkmoth (*Macroglossum stellatarum*). This moth's name refers to its ability to hover in the air while feeding from a flower. Most lepidopterans feed on nectar, but some species feed on other substances, including animal blood or tears.

Incomplete metamorphosis

Hemiptera (85,000 species)



Hemipterans include so-called "true bugs," such as stink bugs, bed bugs, and assassin bugs. (Insects in other orders are sometimes erroneously called bugs.) Hemipterans have two pairs of wings, one pair partly leathery, the other pair membranous. They have piercing or sucking mouthparts and undergo incomplete metamorphosis, as shown in this image of an adult stink bug guarding its offspring (nymphs).

Orthoptera (13,000 species)



Grasshoppers, crickets, and their relatives are mostly herbivorous. They have large hind legs adapted for jumping, two pairs of wings (one leathery, one membranous), and biting or chewing mouthparts. This aptly named spiny devil katydid (*Panacanthus cuspidatus*) has a face and legs specialized for making a threatening display. Male orthopterans commonly make courtship sounds by rubbing together body parts, such as ridges on their hind legs.

Animals as numerous, diverse, and widespread as insects are bound to affect the lives of most other terrestrial organisms, including humans. Insects consume enormous quantities of plant matter; play key roles as predators, parasites, and decomposers; and are an essential source of food for larger animals such as lizards, rodents, and birds. Humans depend on bees, flies, and many other insects to pollinate crops and orchards. In addition, people in many parts of the world eat insects as an important source of protein. On the other hand, insects are carriers for many diseases, including African sleeping sickness (spread by tsetse flies that carry the protist *Trypanosoma*; see Figure 28.9) and malaria (spread by mosquitoes that carry the protist *Plasmodium*; see Figure 23.18 and Figure 28.18).

Insects also compete with humans for food. In parts of Africa, for instance, insects claim about 75% of the crops. In the United States, billions of dollars are spent each year on pesticides. But insect populations often evolve pesticide resistance after short periods of time. Try as we may, not even humans have challenged the preeminence of insects and their arthropod kin. As one prominent entomologist put it: "Bugs are not going to inherit the Earth. They own it now. So we might as well make peace with the landlord."

CONCEPT CHECK 33.4

1. How do nematode and annelid body plans differ?
2. Describe two adaptations that have enabled insects to thrive on land.
3. **MAKE CONNECTIONS** Historically, annelids and arthropods were viewed as closely related because both have body segmentation. Yet DNA sequence data indicate that annelids belong to one clade (Lophotrochozoa) and arthropods to another (Ecdysozoa). Could traditional and molecular hypotheses be tested by studying the *Hox* genes that control body segmentation (see Concept 21.6)? Explain.

For suggested answers, see Appendix A.

CONCEPT 33.5

Echinoderms and chordates are deuterostomes



Sea stars, sea urchins, and other echinoderms (phylum Echinodermata) may seem to have little in common with vertebrates (animals that have a backbone) and other members of phylum Chordata. Nevertheless, DNA evidence indicates that echinoderms and chordates are closely related, with both phyla belonging to the Deuterostomia clade of bilaterian animals. Echinoderms and chordates also share features characteristic of a deuterostome mode of development, such as radial cleavage and formation of the anus from the blastopore (see Figure 32.10). As discussed in Concept 32.4, however, some animal phyla with members that have deuterostome developmental features, including ectoprocts and brachiopods, are not in the deuterostome clade. Hence, despite its name, the clade Deuterostomia is defined primarily by DNA similarities, not developmental similarities.

Echinoderms

Sea stars (commonly called starfish) and most other groups of **echinoderms** (from the Greek *echin*, spiny, and *derma*, skin) are slow-moving or sessile marine animals. Echinoderms have a coelom. A thin epidermis covers an endoskeleton of hard calcareous plates, and most species are prickly from skeletal bumps and spines. Unique to echinoderms is the **water vascular system**, a network of hydraulic canals branching into extensions called **tube feet** that function in locomotion and feeding **(Figure 33.43)**. Sexual reproduction of echinoderms usually involves separate male and female individuals that release their gametes into the water.

Echinoderms descended from bilaterally symmetrical ancestors, yet on first inspection most species seem to have a radially symmetrical form. The internal and external parts of most adult echinoderms radiate from the center, often as five spokes. However, echinoderm larvae have bilateral symmetry. Furthermore, the symmetry of adult echinoderms is not truly radial. For example, the opening (madreporite) of a sea star's water vascular system is not central but shifted to one side.

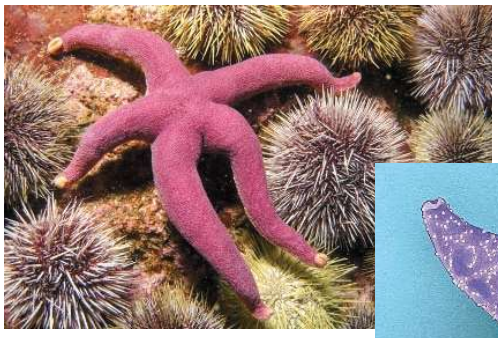
Living echinoderms are divided into five clades.

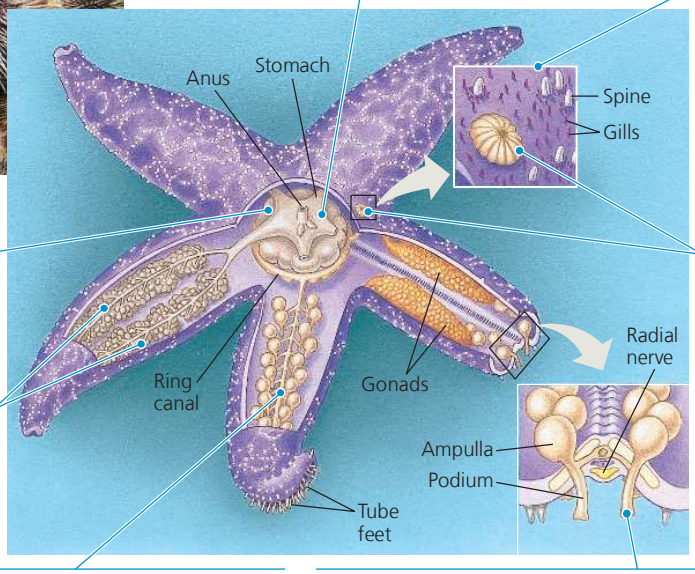
Asteroidea: Sea Stars and Sea Daisies

Sea stars have arms radiating from a central disk; the undersurfaces of the arms bear tube feet. By a combination of muscular and chemical actions, the tube feet can attach to or detach from a substrate. The sea star adheres firmly to rocks or creeps along slowly as its tube feet extend, grip, release, extend, and grip again. Although the base of the tube foot has a flattened disk that resembles a suction cup, the gripping action results from adhesive chemicals, not suction (see Figure 33.43).

Sea stars also use their tube feet to grasp prey, such as clams and oysters. The arms of the sea star embrace the closed bivalve, clinging tightly with their tube feet. The sea star then turns part of its stomach inside out, everting it through its mouth and into the narrow opening between the halves of the bivalve's shell. Next, the digestive system of the sea star secretes juices that begin digesting the mollusc within its own shell. The sea star then brings its stomach back inside its body, where digestion of the mollusc's (now liquefied) body is completed. The ability to begin the digestive process outside of its body allows a sea star to consume bivalves and other prey species that are much larger than its mouth.

Sea stars and some other echinoderms have considerable powers of regeneration. Sea stars can regrow lost arms, and





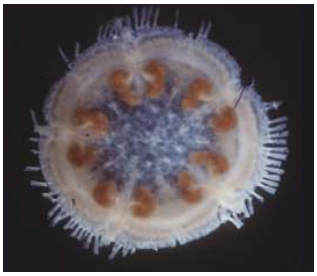
▲ Figure 33.43 Anatomy of a sea star, an echinoderm (top view). In the diagram, the digestive glands, radial canal, and gonads are illustrated in separate arms for clarity, but each is present in every arm. The photograph shows a sea star surrounded by sea urchins, which are also echinoderms.

Mastering Biology Video: Echinoderm Tube Feet

members of one genus can even regrow an entire body from a single arm if part of the central disk remains attached.

The clade Asteroidea, to which sea stars belong, also includes a small group of armless species, the *sea daisies*. Only three species of sea daisies are known, all of which live on submerged wood. A sea daisy's body is typically disk-shaped; it has a five-sided organization and measures less than a centimeter in diameter **(Figure 33.44)**. The edge of the body is ringed with small spines. Sea daisies absorb nutrients through a membrane that surrounds their body.

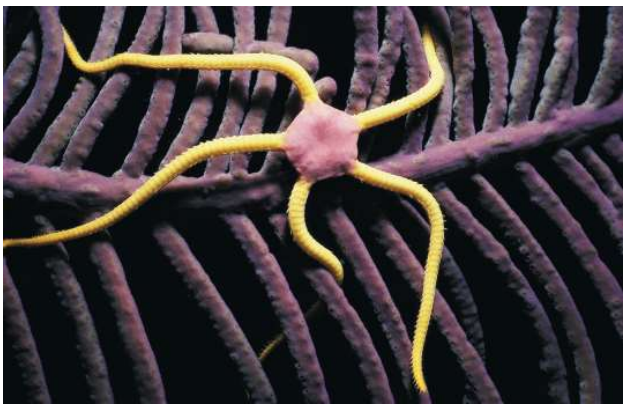
▶ Figure 33.44 A sea daisy (clade Asteroidea).



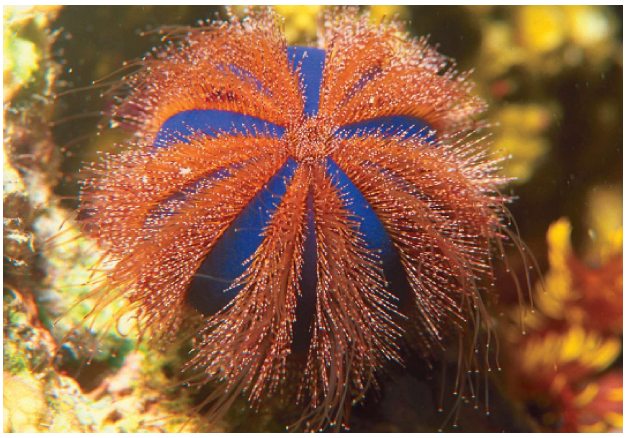
Ophiuroidea: Brittle Stars

Brittle stars have a distinct central disk and long, flexible arms **(Figure 33.45)**. They move primarily by lashing their arms in serpentine movements. The base of a brittle star tube foot lacks the flattened disk found in sea stars but does secrete adhesive chemicals. Hence, like sea stars and other

▼ Figure 33.45 A brittle star (clade Ophiuroidea).



▼ **Figure 33.46** **A sea urchin (clade Echinoidea).**



echinoderms, brittle stars can use their tube feet to grip substrates. Some species are suspension feeders; others are predators or scavengers.

Echinoidea: Sea Urchins and Sand Dollars

Sea urchins and sand dollars have no arms, but they do have five radially arranged groups of tube feet that function in slow movement. Sea urchins also have muscles that pivot their long spines, which aid in locomotion as well as protection **(Figure 33.46)**. A sea urchin's mouth, located on its underside, is ringed by highly complex, jaw-like structures that are well adapted to eating seaweed. Sea urchins are roughly spherical, whereas sand dollars are flat disks.

Crinoidea: Sea Lilies and Feather Stars

Sea lilies live attached to the substrate by a stalk; feather stars crawl about by using their long, flexible arms. Both use their arms in suspension feeding. The arms encircle the mouth, which is directed upward, away from the substrate **(Figure 33.47)**. Crinoidea is an ancient group whose

▼ **Figure 33.47** **A feather star (clade Crinoidea).**



▼ **Figure 33.48** **A sea cucumber (clade Holothuroidea).**



morphology has changed little over the course of evolution; fossilized sea lilies some 500 million years old are extremely similar to present-day members of the clade.

Holothuroidea: Sea Cucumbers

On casual inspection, sea cucumbers do not look much like other echinoderms. They lack spines, and their endoskeleton is much reduced. They are also elongated in their oral-aboral axis, giving them the shape for which they are named and further disguising their relationship to sea stars and sea urchins **(Figure 33.48)**. Closer examination, however, reveals that sea cucumbers have five radially arranged sections of tube feet, as in other echinoderms. Some of the tube feet around the mouth are developed as feeding tentacles.

Chordates

Phylum Chordata consists of two basal groups of invertebrates, the lancelets and the tunicates, as well as the vertebrates. Chordates are bilaterally symmetrical animals with a coelom and segmented bodies. The close relationship between echinoderms and chordates does not mean that one phylum evolved from the other. In fact, echinoderms and chordates have evolved independently of one another for over 500 million years. We will trace the phylogeny of chordates in Chapter 34, focusing on the history of vertebrates.

CONCEPT CHECK 33.5

1. How do sea star tube feet attach to substrates?
2. **WHAT IF?** The insect *Drosophila melanogaster* and the nematode *Caenorhabditis elegans* are prominent model organisms. Are these species the most appropriate invertebrates for making inferences about humans and other vertebrates? Explain.
3. **MAKE CONNECTIONS** Describe how the features and diversity of echinoderms illustrate the unity of life, the diversity of life, and the match between organisms and their environments (see Concept 22.2).

For suggested answers, see Appendix A.

33 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

This table recaps the animal groups surveyed in this chapter.

Key Concept	Phylum	Description
CONCEPT 33.1 **Sponges are basal animals that lack tissues** *(pp. 690–691)* ? *Lacking tissues and organs, how do sponges accomplish tasks such as gas exchange, nutrient transport, and waste disposal?*	Porifera (sponges)	Lack tissues; have choanocytes (collar cells—flagellated cells that ingest bacteria and tiny food particles)
CONCEPT 33.2 **Cnidarians are an ancient phylum of eumetazoans** *(pp. 691–693)* ? *Describe the cnidarian body plan and its two major variations.*	Cnidaria (hydras, jellies, sea anemones, corals)	Unique stinging structures (nematocysts) housed in specialized cells (cnidocytes); diploblastic; radially symmetrical; gastrovascular cavity (digestive compartment with a single opening)
CONCEPT 33.3 **Lophotrochozoans, a clade identified by molecular data, have the widest range of animal body forms** *(pp. 694–705)* ? *Is the lophotrochozoan clade united by unique morphological features shared by all of its members? Explain.*	Platyhelminthes (flatworms)	No body cavity; dorsoventrally flattened; gastrovascular cavity or no digestive tract
	Syndermata (rotifers and acanthocephalans)	Hemocoel; rotifers have alimentary canal (digestive tube with mouth and anus) and jaws (trophi); acanthocephalans are parasites of vertebrates
	Ectoprocta and Brachiopoda	Coelom; have lophophores (feeding structures bearing ciliated tentacles)
	Mollusca (clams, snails, squids)	Hemocoel; reduced coelom; three main body parts (muscular foot, visceral mass, mantle); most have hard shell made of calcium carbonate
	Annelida (segmented worms)	Coelom; body wall and internal organs are segmented (except digestive tract, which is unsegmented)
CONCEPT 33.4 **Ecdysozoans are the most species-rich animal group** *(pp. 705–713)* ? *Describe some ecological roles of nematodes and arthropods.*	Nematoda (roundworms)	Hemocoel; cylindrical body with tapered ends; no circulatory system; undergo ecdysis
	Arthropoda (spiders, centipedes, crustaceans, and insects)	Hemocoel; reduced coelom. Have segmented body, jointed appendages, and exoskeleton made of protein and chitin
CONCEPT 33.5 **Echinoderms and chordates are deuterostomes** *(pp. 713–715)* ? *You've read that echinoderms and chordates are closely related and have evolved independently for over 500 million years. Explain how both of these statements can be correct.*	Echinodermata (sea stars, sea urchins)	Coelom; bilaterally symmetrical larvae and five-part body organization as adults; unique water vascular system; endoskeleton
	Chordata (lancelets, tunicates, vertebrates)	Coelom; have notochord; dorsal, hollow nerve cord; pharyngeal slits; post-anal tail (see Figure 34.3)

Metazoa; Eumetazoa; Bilateria; Lophotrochozoa; Ecdysozoa; Deuterostomia

TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

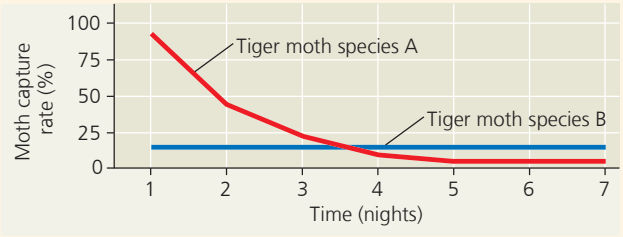
1. A land snail, a clam, and an octopus all share
   (A) a mantle. (C) gills.
   (B) a radula. (D) distinct cephalization.
2. Which phylum is characterized by animals that have a segmented body?
   (A) Cnidaria (C) Arthropoda
   (B) Platyhelminthes (D) Mollusca
3. The water vascular system of echinoderms
   (A) functions as a circulatory system that distributes nutrients to body cells.
   (B) functions in locomotion and feeding.
   (C) is bilateral in organization, even though the adult animal is not bilaterally symmetrical.
   (D) moves water through the animal's body during filter feeding.
4. Which of the following combinations of phylum and description is correct?
   (A) Echinodermata—radial symmetry as a larva, coelom
   (B) Nematoda—roundworms, internal skeleton
   (C) Platyhelminthes—flatworms, gastrovascular cavity, no body cavity
   (D) Porifera—gastrovascular cavity, coelom

Levels 3-4: Applying/Analyzing

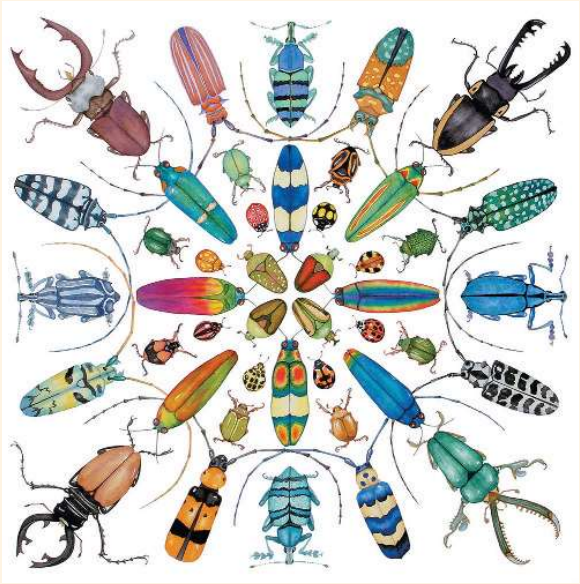
5. In Figure 33.1, which two main clades branch from the most recent common ancestor of the eumetazoans?
   (A) Porifera and Cnidaria
   (B) Lophotrochozoa and Ecdysozoa
   (C) Cnidaria and Bilateria
   (D) Deuterostomia and Bilateria
6. **MAKE CONNECTIONS** In Figure 33.7, assume that the two medusae shown at step 4 were produced by one polyp colony. Review Concept 12.1 and Concept 13.3, and then use your understanding of mitosis and meiosis to select which of the following is true.
   (A) Both the medusae and the gametes are genetically identical.
   (B) Neither the medusae nor the gametes are genetically identical.
   (C) The medusae are not genetically identical but the gametes are genetically identical.
   (D) The medusae are genetically identical but the gametes differ genetically.

Levels 5-6: Evaluating/Creating

7. **EVOLUTION CONNECTION • INTERPRET THE DATA** Based on Figure 32.11, draw a phylogenetic tree of Bilateria that includes the ten phyla of bilaterians discussed in detail in this chapter. Label each branch that leads to a phylum with a C, H, HC, or N, depending on whether members of the phylum have a coelom only (C), hemocoel only (H), hemocoel and reduced coelom (HC), or no body cavity (N). Use your labeled tree to answer the following questions. (a) For each of the three major clades of bilaterians, what (if anything) can be inferred about whether the common ancestor of the clade had a coelom? (b) To what extent has the presence of a coelom in animals changed over the course of evolution?
8. **SCIENTIFIC INQUIRY** Bats emit ultrasonic sounds and then use the returning echoes of those sounds to locate and capture flying insects, such as moths, in the dark. In response to bat attacks, some tiger moths make ultrasonic clicks of their own. Researchers hypothesize that tiger moth clicks likely either (1) jam the bat's sonar or (2) warn the bat about the moth's toxic chemical defenses. The graph below shows two patterns observed in studies of moth capture rates over time.



   Bats in these experiments were "naive," meaning that prior to the study the bats had not previously hunted tiger moths. Indicate whether the results support hypothesis (1), hypothesis (2), or both. Explain why the researchers used naive bats in this study.
9. **WRITE ABOUT A THEME: ORGANIZATION** Write a short essay (100–150 words) that explains how the structure of the digestive tract in different invertebrate groups affects the size of the organisms that they can eat.
10. **SYNTHESIZE YOUR KNOWLEDGE**



   Collectively, do these beetles and all other invertebrate species combined form a monophyletic group? Explain your answer and provide an overview of the evolutionary history of invertebrate life.

For selected answers, see Appendix A.

34 The Origin and Evolution of Vertebrates

KEY CONCEPTS

34.1 Chordates have a notochord and a dorsal, hollow nerve cord *p. 719*

34.2 Vertebrates are chordates that have a backbone *p. 722*

34.3 Gnathostomes are vertebrates that have jaws *p. 725*

34.4 Tetrapods are gnathostomes that have limbs *p. 730*

34.5 Amniotes are tetrapods that have a terrestrially adapted egg *p. 734*

34.6 Mammals are amniotes that have hair and produce milk *p. 741*

34.7 Humans are mammals that have a large brain and bipedal locomotion *p. 748*

Study Tip

Make a table: Humans are mammals—and we are also amniotes, tetrapods, lobe-fins, osteichthyans, gnathostomes, vertebrates, and chordates (see Figure 34.2). As you read the chapter, list derived characters for these clades and describe whether these traits have been retained, modified, or lost in the human lineage.

Clade	Derived characters	Found in humans?
Chordates	Notochord	Modified (gelatinous disks between vertebrae)
	Post-anal tail	Lost

Go to Mastering Biology

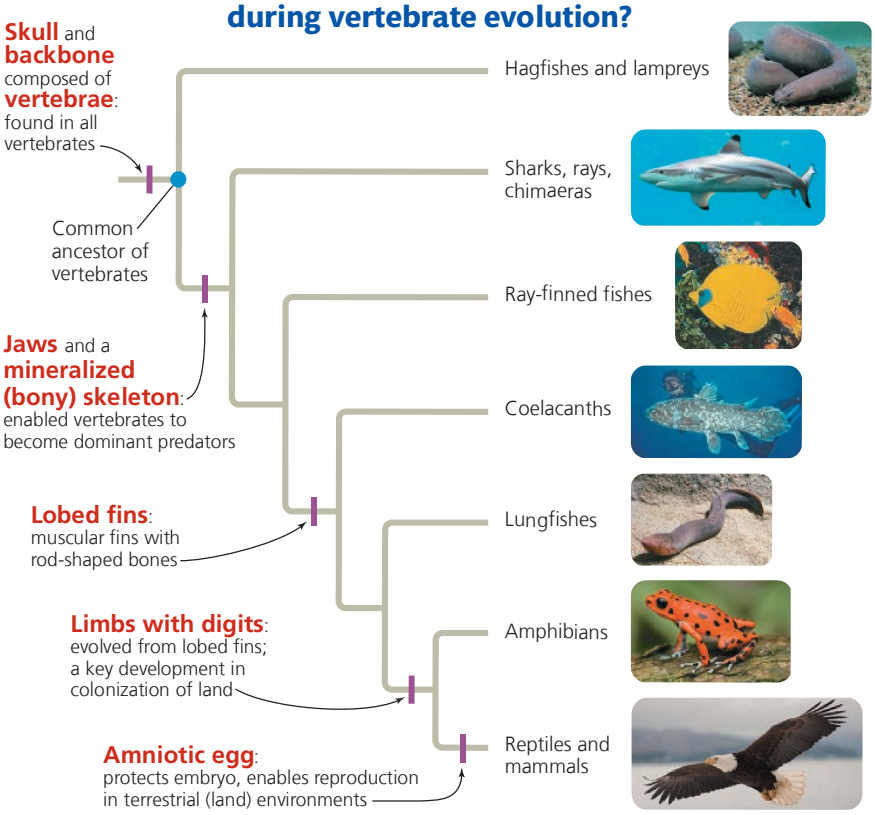
For Students (in eText and Study Area)
- Get Ready for Chapter 34
- Video: Sea Horse Camouflage
- HHMI Video: Great Transitions: The Origins of Humans

For Instructors to Assign (in Item Library)
- Tutorial: Chordates
- Problem-Solving Exercise: Declining Amphibian Populations



Figure 34.1 Small and slender, this inconspicuous species (*Myllokunmingia fengjiaoa*) lived in the ocean 530 million years ago, along with an immense variety of dangerous and well-defended invertebrate animals. Although lacking claws or armor, this ancient species was closely related to one of the most successful groups of animals on Earth: the vertebrates, animals with a backbone.

What are some key characteristics that have appeared during vertebrate evolution?



There are more than 60,000 species of **vertebrates**, animals with a backbone. This is a relatively small number compared to, say, the 1 million insect species on Earth. But what vertebrates lack in number of species, they make up for in *disparity*, varying enormously in characteristics such as body mass. Vertebrates include the heaviest animals ever to walk on land, plant-eating dinosaurs that were as massive as 40,000 kg (heavier than 13 pickup trucks). The biggest animal ever to exist on Earth is also a vertebrate—the blue whale, which can exceed 100,000 kg. On the other end of the spectrum, the fish *Schindleria brevipinguis* is just 8.4 mm long and has a mass roughly 100 billion times smaller than that of a blue whale.

In this chapter, we will track the origin and evolution of the vertebrate body plan, from a notochord to a head to a mineralized skeleton to limbs with digits (such as toes). We'll also explore the major groups of vertebrates (both living and extinct), as well as the evolutionary history of our own species—*Homo sapiens*.

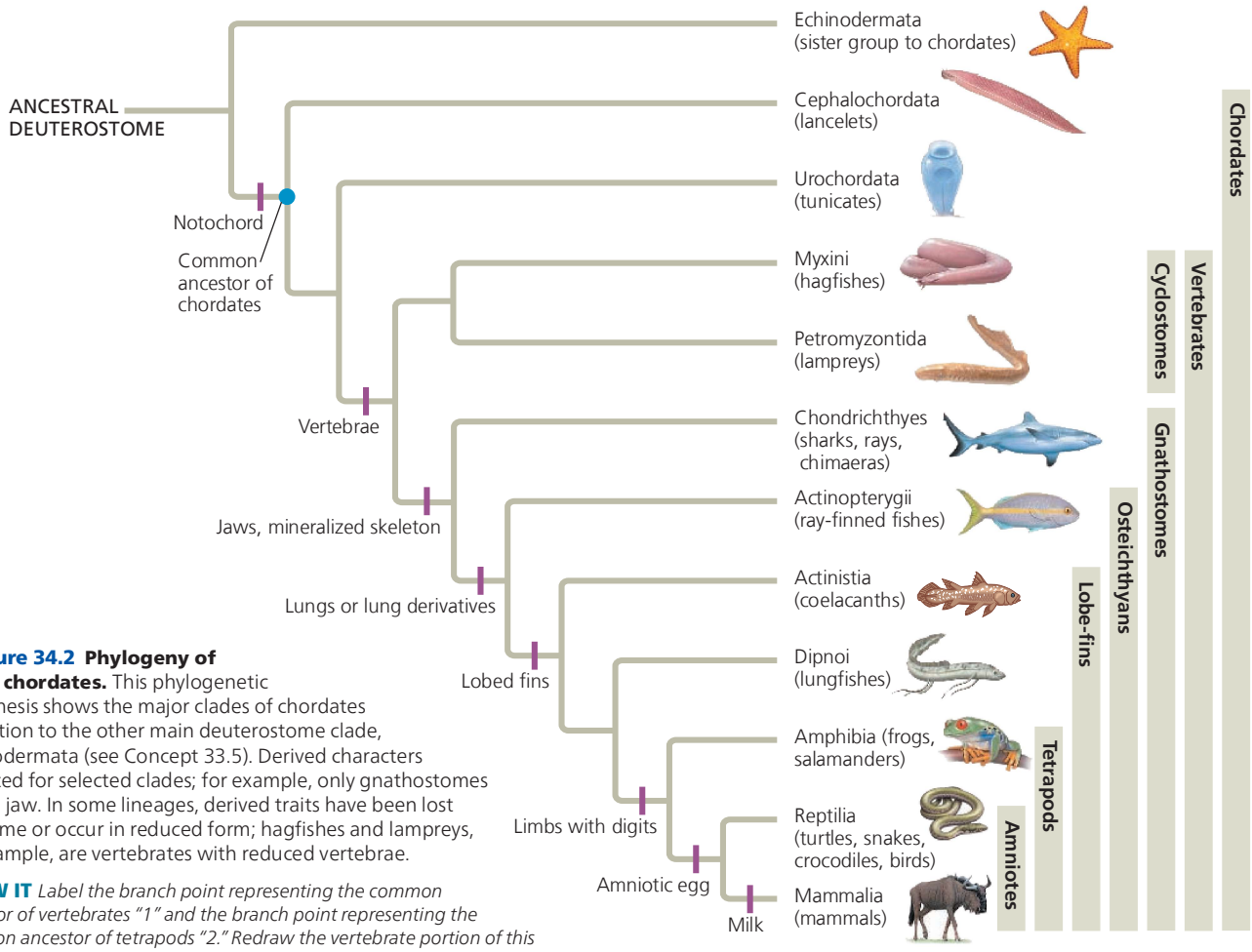
CONCEPT 34.1

Chordates have a notochord and a dorsal, hollow nerve cord

Vertebrates are members of the phylum Chordata, the chordates. **Chordates** are bilaterian (bilaterally symmetrical) animals, and within Bilateria, they belong to the clade of animals known as Deuterostomia (see Figure 32.11). As shown in **Figure 34.2**, there are two groups of invertebrate deuterostomes that are more closely related to vertebrates than they are to other invertebrates: the cephalochordates and the urochordates. Thus, along with the vertebrates, these two invertebrate groups are classified within the chordates.

Derived Characters of Chordates

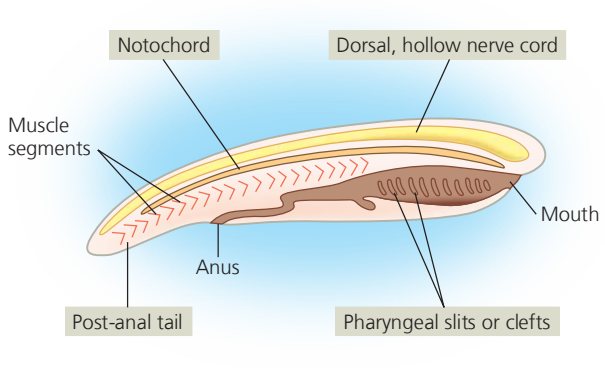
All chordates share a set of derived characters, though many species possess some of these traits only during embryonic



▶ **Figure 34.2 Phylogeny of living chordates.** This phylogenetic hypothesis shows the major clades of chordates in relation to the other main deuterostome clade, Echinodermata (see Concept 33.5). Derived characters are listed for selected clades; for example, only gnathostomes have a jaw. In some lineages, derived traits have been lost over time or occur in reduced form; hagfishes and lampreys, for example, are vertebrates with reduced vertebrae.

DRAW IT *Label the branch point representing the common ancestor of vertebrates "1" and the branch point representing the common ancestor of tetrapods "2." Redraw the vertebrate portion of this tree by rotating its branches around these two branch points. Use the redrawn tree to explain why it is* not *correct to represent evolution as a sequence of events "leading to" humans and other mammals.*

▼ **Figure 34.3 Chordate characteristics.** All chordates possess the four highlighted structural trademarks at some point during their development.



development. **Figure 34.3** illustrates four key characters of chordates: a notochord; a dorsal, hollow nerve cord; pharyngeal slits or clefts; and a muscular, post-anal tail.

Notochord

Chordates are named for a skeletal structure, the notochord, present in all chordate embryos as well as in some adult chordates. The **notochord** is a longitudinal, flexible rod located between the digestive tube and the nerve cord. It is composed of large, fluid-filled cells encased in fairly stiff, fibrous tissue. The notochord provides skeletal support throughout most of the length of a chordate, and in larvae or adults that retain it, it also provides a firm but flexible structure against which muscles can work during swimming. In most vertebrates, a more complex, jointed skeleton develops around the ancestral notochord, and the adult retains only remnants of the embryonic notochord. In humans, for example, the notochord is reduced and forms part of the gelatinous disks sandwiched between the vertebrae.

Dorsal, Hollow Nerve Cord

The nerve cord of a chordate embryo develops from a plate of ectoderm that rolls into a neural tube located dorsal to the notochord. The resulting dorsal, hollow nerve cord is unique to chordates. Other animal phyla have solid nerve cords, and in most cases they are ventrally located. The nerve cord of a chordate embryo develops into the central nervous system: the brain and spinal cord.

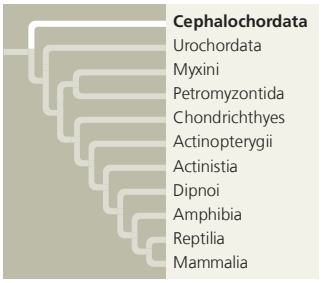
Pharyngeal Slits or Clefts

The digestive tube of chordates extends from the mouth to the anus. The region just posterior to the mouth is the pharynx. In all chordate embryos, a series of arches separated by grooves forms along the outer surface of the pharynx. In most chordates, these grooves (known as **pharyngeal clefts**) develop into slits that open into the pharynx. These **pharyngeal slits** allow water entering the mouth to exit the body without passing through the entire digestive tract. Pharyngeal slits function as suspension-feeding devices in many invertebrate chordates. In vertebrates (with the exception of vertebrates with limbs, the *tetrapods*), these slits and the pharyngeal arches that support them have been modified for gas exchange and are called gills. In tetrapods, the pharyngeal clefts do not develop into slits. Instead, the pharyngeal arches that surround the clefts develop into parts of the ear and other structures in the head and neck.

Muscular, Post-Anal Tail

Chordates have a tail that extends posterior to the anus, although in many species it is greatly reduced during embryonic development. In contrast, most nonchordates have a digestive tract that extends nearly the whole length of the body. The chordate tail contains skeletal elements and muscles, and it helps propel many aquatic species in the water.

Lancelets

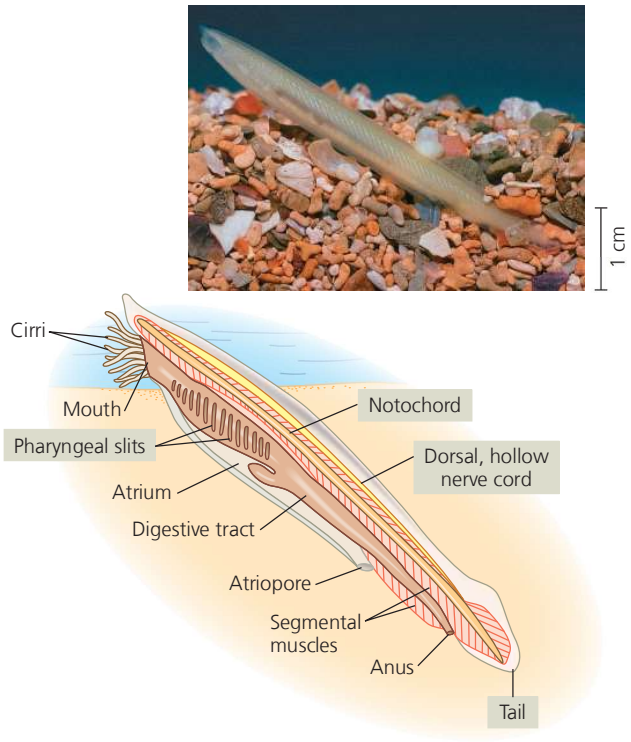


The sister group to all other living chordates is the group of animals called **lancelets** (Cephalochordata), which get their name from their bladelike shape **(Figure 34.4)**. As larvae, lancelets develop a notochord; a dorsal, hollow nerve cord; numerous pharyngeal slits; and a post-anal tail. The larvae feed on plankton in the water column, alternating between upward swimming and passive sinking. As the larvae sink, they trap plankton and other suspended particles in their pharynx.

Adult lancelets can reach 6 cm in length. They retain key chordate traits, closely resembling the generalized chordate shown in Figure 34.3. Following metamorphosis, an adult lancelet swims down to the seafloor and wriggles backward into the sand, leaving only its anterior end exposed. Cilia draw seawater into the lancelet's mouth. A net of mucus secreted across the pharyngeal slits removes tiny food particles as the water passes through the slits, and the trapped food enters the intestine. The pharynx and pharyngeal slits play a minor role in gas exchange, which occurs mainly across the external body surface.

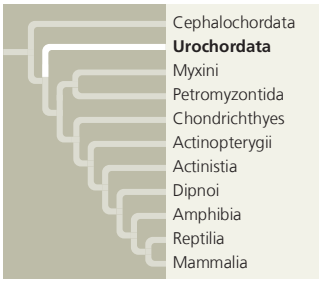
A lancelet frequently leaves its burrow to swim to a new location. Though feeble swimmers, these invertebrate chordates display, in a simple form, the swimming mechanism of fishes. Coordinated contraction of muscles arranged like rows of chevrons (>>>>) along the sides of the notochord flexes the notochord, producing side-to-side undulations that thrust the body forward. This serial arrangement of muscles is evidence of the lancelet's segmentation. The muscle segments develop from blocks of mesoderm called *somites*, which are found along each side of the notochord in all chordate embryos.

▼ Figure 34.4 The lancelet *Branchiostoma*, a cephalochordate. This small invertebrate displays all four main chordate characters. Water enters the mouth and passes through the pharyngeal slits into the atrium, a chamber that vents to the outside via the atriopore; large particles are blocked from entering the mouth by tentacle-like cirri. The serially arranged segmental muscles produce the lancelet's wavelike swimming movements.



Globally, lancelets are rare, but in a few areas (such as Tampa Bay, on the Florida coast), they may reach densities of more than 5,000 individuals per square meter.

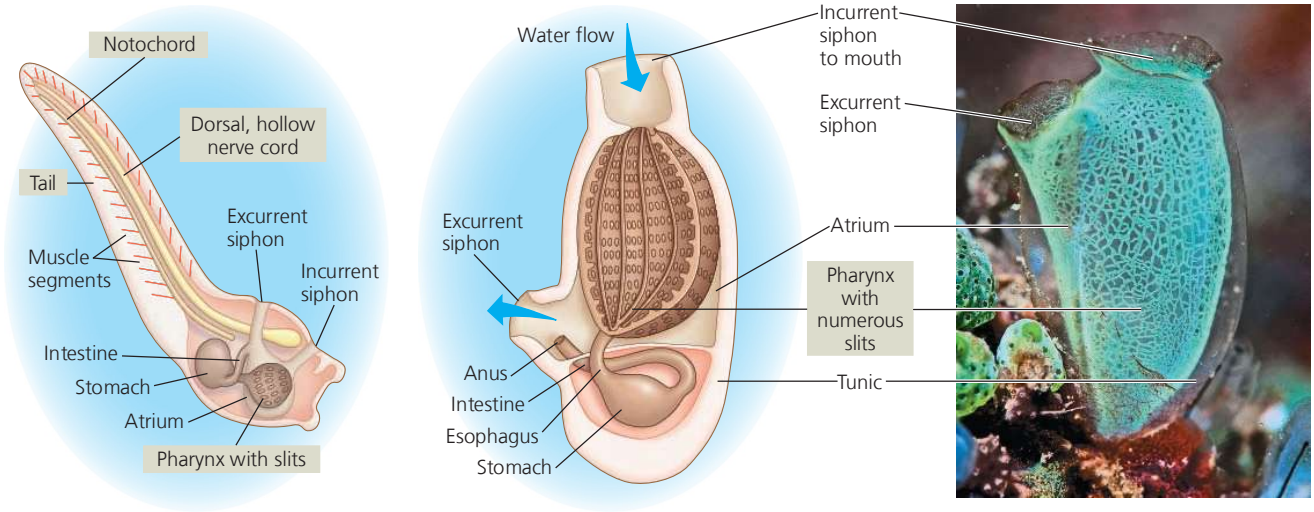
Tunicates



Recent molecular studies indicate that the **tunicates** (Urochordata) are more closely related to other chordates than are lancelets. The chordate characters of tunicates are most apparent during their larval stage, which may be as brief as a few minutes **(Figure 34.5a)**. In many species, the larva uses its tail muscles and notochord to swim through water in search of a suitable substrate on which it can settle, guided by cues it receives from light- and gravity-sensitive cells.

Once a tunicate has settled on a substrate, it undergoes a radical metamorphosis in which many of its chordate characters disappear. Its tail and notochord are resorbed; its nervous system degenerates; and its remaining organs rotate 90°. As an adult, a tunicate draws in water through an incurrent siphon; the water then passes through the pharyngeal slits into a chamber called the atrium and exits through an excurrent siphon **(Figure 34.5b** and **c)**. Food particles are filtered from the water by a mucous net and transported by cilia to the esophagus. The anus empties into the excurrent siphon. Some tunicate species shoot a jet of water through their excurrent siphon when attacked, earning them the informal name of "sea squirts."

▼ Figure 34.5 A tunicate, a urochordate.



(a) A tunicate larva is a free-swimming but nonfeeding "tadpole" in which all four main characters of chordates are evident.

(b) In the adult, prominent pharyngeal slits function in suspension feeding, but other chordate characters are not obvious.

(c) An adult tunicate, or sea squirt, is a sessile animal (photo is approximately life-sized).

The loss of chordate characters in the adult stage of tunicates appears to have occurred after the tunicate lineage branched off from other chordates. Even the tunicate larva appears to be highly derived. For example, tunicates have nine *Hox* genes, whereas all other chordates studied to date—including the early-diverging lancelets—share a set of 13 *Hox* genes. The apparent loss of four *Hox* genes indicates that the chordate body plan of a tunicate larva is built using a different set of genetic controls than other chordates.

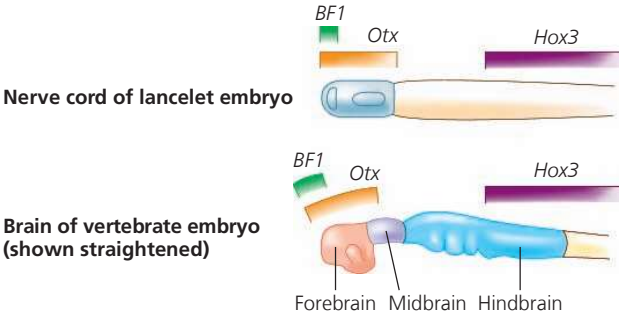
Early Chordate Evolution

Although lancelets and tunicates are relatively obscure animals, they occupy key positions in the history of life and can provide clues about the evolutionary origin of vertebrates. For example, as you have read, lancelets display key chordate characters as adults, and their lineage branches from the base of the chordate phylogenetic tree. These findings suggest that the ancestral chordate may have looked something like a lancelet—that is, it had an anterior end with a mouth; a notochord; a dorsal, hollow nerve cord; pharyngeal slits; and a post-anal tail.

Research on lancelets has also revealed important clues about the evolution of the chordate brain. Rather than a full-fledged brain, lancelets have only a slightly swollen tip on the anterior end of their dorsal nerve cord **(Figure 34.6)**. But the same *Hox* genes that organize major regions of the forebrain, midbrain, and hindbrain of vertebrates express themselves in a corresponding pattern in this small cluster of cells in the lancelet's nerve cord. This suggests that the vertebrate brain is an elaboration of an ancestral structure similar to the lancelet's simple nerve cord tip.

As for tunicates, several of their genomes have been completely sequenced and can be used to identify genes likely to have been present in early chordates. Researchers have suggested that ancestral chordates had genes associated with vertebrate organs such as the heart and thyroid gland. These genes are found in tunicates and vertebrates but are absent from nonchordate invertebrates. Another recent study found that tunicates (but not lancelets) have embryonic cells that have some of the characteristics of the *neural crest*, a derived trait found in all vertebrates (see Figure 34.7). This suggests that embryonic cells similar to those in tunicates may represent an intermediate cell population from which the vertebrate neural crest evolved.

▼ Figure 34.6 Expression of developmental genes in lancelets and vertebrates. *Hox* genes (including *BF1*, *Otx*, and *Hox3*) control the development of major regions of the vertebrate brain. These genes are expressed in the same anterior-to-posterior order in lancelets and vertebrates. Each colored bar is positioned above the portion of the brain whose development that gene controls.



MAKE CONNECTIONS *What do these expression patterns and those in Figure 21.19 indicate about* Hox *genes and their evolution?*

CONCEPT CHECK 34.1

1. Identify the four derived characters that all chordates have at some point during their life.
2. You are a chordate, yet you lack most of the main derived characters of chordates. Explain.
3. **VISUAL SKILLS** Based on the phylogenetic tree in Figure 34.2, predict which vertebrate groups should have lungs or lung derivatives. Explain.

For suggested answers, see Appendix A.

CONCEPT 34.2

Vertebrates are chordates that have a backbone

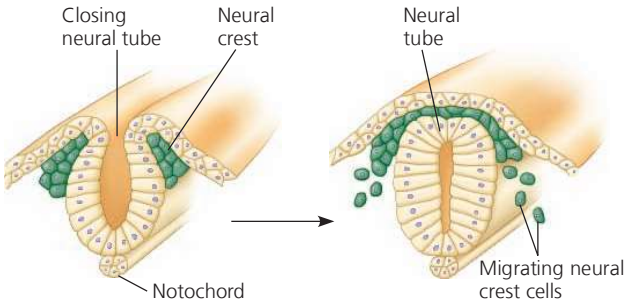
During the Cambrian period, half a billion years ago, a lineage of chordates gave rise to vertebrates. With a skeletal system and a more complex nervous system than that of their ancestors, vertebrates became more efficient at two essential tasks: capturing food and avoiding being eaten.

Derived Characters of Vertebrates

Living vertebrates share a set of derived characters that distinguish them from other chordates. For example, as a result of gene duplication, vertebrates possess two or more sets of *Hox* genes (lancelets and tunicates have only one). Other important families of genes that produce transcription factors and signaling molecules are also duplicated in vertebrates. The resulting additional genetic complexity may be associated with innovations in the vertebrate nervous system and skeleton, including the development of a skull and a backbone composed of vertebrae. In some vertebrates, the vertebrae are little more than small prongs of cartilage arrayed dorsally along the notochord. In the majority of vertebrates, however, the vertebrae enclose the spinal cord and have taken over the mechanical roles of the notochord.

Another feature unique to vertebrates is the **neural crest**, a collection of cells that appears along the edges of the closing neural tube of an embryo **(Figure 34.7)**. Neural crest cells disperse throughout the embryo, where they give rise to a variety of structures, including teeth, some of the bones and cartilage of the skull, several types of neurons, and the sensory capsules in which eyes and other sense organs develop.

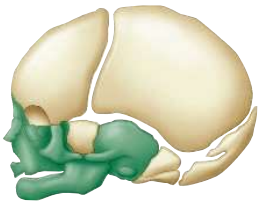
▼ Figure 34.7 The neural crest, embryonic source of many unique vertebrate traits.



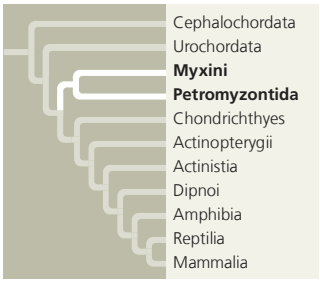
(a) The neural crest consists of bilateral bands of cells near the margins of the embryonic folds that form the neural tube.

(b) Neural crest cells migrate to distant sites in the embryo.

(c) The migrating neural crest cells give rise to some of the anatomical structures unique to vertebrates, including some of the bones and cartilage of the skull. (A fetal human skull is depicted here.)



Hagfishes and Lampreys



The **hagfishes** (Myxini) and the **lampreys** (Petromyzontida) are the only lineages of living vertebrates whose members lack jaws. Unlike most vertebrates, lampreys and hagfishes also do not have a backbone. Even so, lampreys are classified as vertebrates because they have rudimentary vertebrae (composed of cartilage, not bone). The hagfishes, in contrast, once were thought to lack vertebrae altogether; hence, they were classified as invertebrate chordates closely related to vertebrates.

In the past few years, however, this interpretation has changed. Recent research has shown that hagfishes, like lampreys, have rudimentary vertebrae. In addition, a series of molecular phylogenetic studies have supported the hypothesis that hagfishes are vertebrates. Molecular analyses also indicate that hagfishes and lampreys are sister groups, as shown in Figure 34.2. Together, the hagfishes and lampreys form a clade of living jawless vertebrates, the **cyclostomes**. (All other vertebrates have jaws and make up a much larger clade, the gnathostomes, which we will discuss in Concept 34.3.)

Hagfishes

The hagfishes are jawless vertebrates that have highly reduced vertebrae and a skull that is made of cartilage. They swim in a snakelike fashion by using their segmental muscles to exert

▼ Figure 34.8 A hagfish.



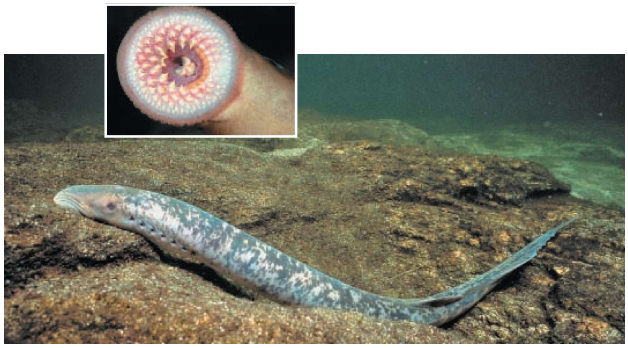
force against their notochord, which they retain in adulthood as a strong, flexible rod of cartilage. Hagfishes have a small brain, eyes, ears, and a nasal opening that connects with the pharynx. Their mouths contain tooth-like formations made of the protein keratin.

All of the 30 living species of hagfishes are marine. Measuring up to 60 cm in length, most are bottom-dwelling scavengers **(Figure 34.8)** that feed on worms and sick or dead fish. Rows of slime glands on a hagfish's flanks secrete a substance that absorbs water, forming a slime that may repel other scavengers when a hagfish is feeding. When attacked by a predator, a hagfish can produce several liters of slime in less than a minute. The slime coats the gills of the attacking fish, sending it into retreat or even suffocating it. Biologists and engineers are investigating the properties of hagfish slime as a model for developing a space-filling gel that could be used, for instance, to stop bleeding during surgery.

Lampreys

The second group of living jawless vertebrates, the lampreys, consists of about 38 species inhabiting various marine and freshwater environments **(Figure 34.9)**. Some are parasites

▼ Figure 34.9 A sea lamprey. Parasitic lampreys use their mouth (inset) and tongue to bore a hole in the side of a fish. The lamprey then ingests the blood and other tissues of its host.



that feed by clamping their round, jawless mouth onto the flank of a live fish, their "host." Parasitic lampreys use their rasping mouth and tongue to penetrate the skin of the fish and ingest the fish's blood and other tissues.

As larvae, lampreys live in freshwater streams. The larva is a suspension feeder that resembles a lancelet and spends much of its time partially buried in sediment. About 20 species of lampreys are not parasitic. These species feed only as larvae; following several years in streams, they mature sexually, reproduce, and die within a few days. In contrast, parasitic species of lampreys migrate to the sea or lakes as they mature into adults. One such parasite, the sea lamprey (*Petromyzon marinus*), has invaded the Great Lakes over the past 170 years and devastated a number of fisheries there.

The skeleton of lampreys is made of cartilage. Unlike the cartilage found in most vertebrates, lamprey cartilage contains no collagen. Instead, it is a stiff matrix of other proteins. The notochord of lampreys persists as the main axial skeleton in the adult, as it does in hagfishes. However, lampreys also have a flexible sheath around their rodlike notochord. Along the length of this sheath, pairs of cartilaginous projections related to vertebrae extend dorsally, partially enclosing the nerve cord.

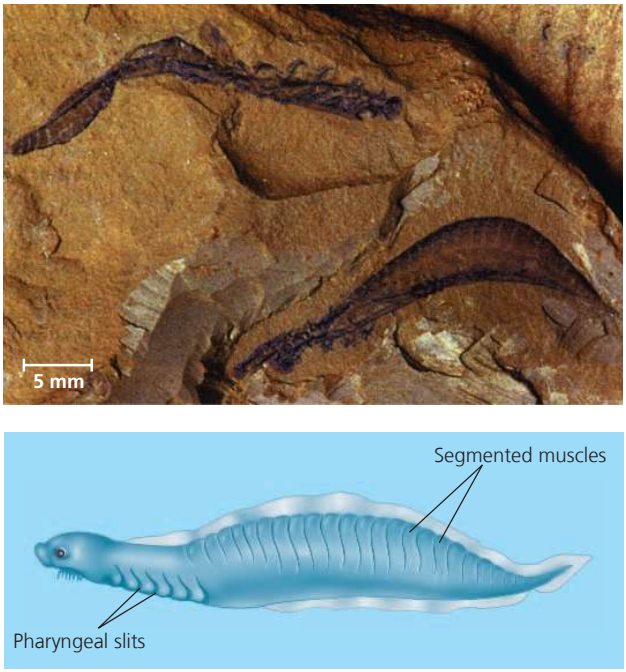
Early Vertebrate Evolution

In the late 1990s, paleontologists working in China discovered a vast collection of fossils of early chordates that appear to straddle the transition to vertebrates. The fossils were formed 530 million years ago during the Cambrian explosion, when many animal groups were undergoing rapid diversification (see Concept 32.2).

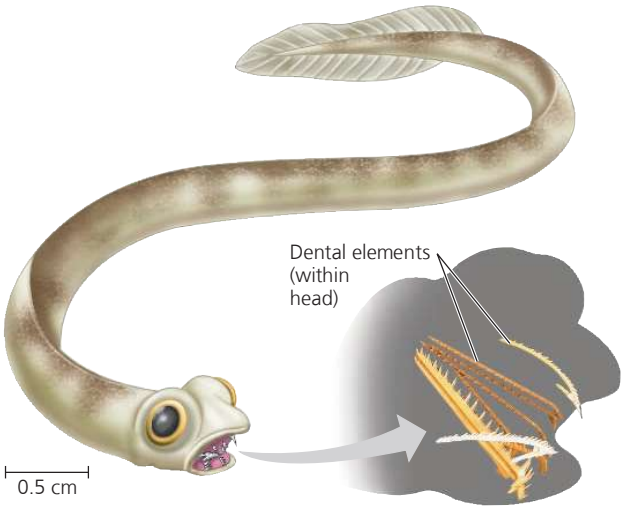
The most primitive of the fossils are the 3-cm-long *Haikouella* **(Figure 34.10)**. In many ways, *Haikouella* resembled a lancelet. Its mouth structure indicates that, like lancelets, it probably was a suspension feeder. However, *Haikouella* also had some of the characters of vertebrates. For example, it had a well-formed brain, small eyes, and muscle segments along the body, as do the vertebrate fishes. Unlike the vertebrates, however, *Haikouella* did not have a skull or ear organs, suggesting that these characters emerged with further innovations to the chordate nervous system. (The earliest "ears" were organs for maintaining balance, a function still performed by the ears of humans and other living vertebrates.)

Early signs of a skull can be seen in *Myllokunmingia* (see Figure 34.1). About the same size as *Haikouella, Myllokunmingia* had ear capsules and eye capsules, parts of the skull that surround these organs. Based on these and other characters, *Myllokunmingia* is considered the first chordate to have a head. The origin of a head—consisting of a brain at the anterior end of the dorsal nerve cord, eyes and other sensory organs, and a skull—enabled chordates to coordinate more complex movement and feeding behaviors. Although it had a head, *Myllokunmingia* lacked vertebrae and hence is not classified as a vertebrate.

▼ Figure 34.10 Fossil of an early chordate. Discovered in 1999 in southern China, *Haikouella* had eyes and a brain but lacked a skull, a trait found in vertebrates. The organism's color in the drawing is fanciful.



▼ Figure 34.11 A conodont. Conodonts were early jawless vertebrates that lived from 500 million to 200 million years ago. Unlike hagfishes and lampreys, conodonts had mineralized mouthparts, which they used for either predation or scavenging.



The earliest fossils of vertebrates date to 500 million years ago and include those of **conodonts** **(Figure 34.11)**, a group of slender, soft-bodied vertebrates that lacked jaws and whose internal skeleton was composed of cartilage. Conodonts had large eyes, which they may have used in locating prey that

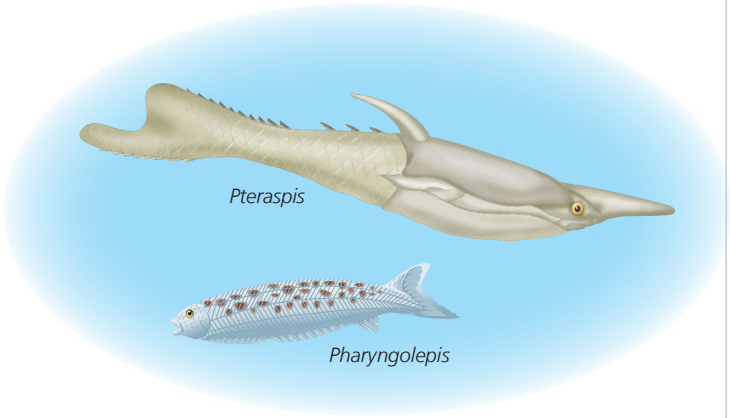
were then impaled on a set of barbed hooks at the anterior end of their mouth (see Figure 34.11). These hooks were made of dental tissues that were *mineralized*—hardened by the incorporation of minerals such as calcium. The food was then passed back to the pharynx, where a different set of dental elements sliced and crushed the food.

Conodonts were extremely abundant for 300 million years. Their fossilized dental elements are so plentiful that they have been used for decades by petroleum geologists as guides to the age of rock layers in which they search for oil.

Vertebrates with additional innovations emerged during the Ordovician, Silurian, and Devonian periods (485–359 million years ago). These vertebrates had paired fins and, as in lampreys, an inner ear with two semicircular canals that provided a sense of balance. Like conodonts, these vertebrates lacked jaws, but they had a muscular pharynx, which they may have used to suck in bottom-dwelling organisms or detritus. They were also armored with mineralized bone, which covered varying amounts of their body and may have offered protection from predators **(Figure 34.12)**. There were many species of these jawless, armored swimming vertebrates, but they all became extinct by the end of the Devonian.

Finally, note that the human skeleton is heavily mineralized bone, whereas cartilage plays a fairly minor role. But a bony internal skeleton was a relatively late development in the history of vertebrates. Instead, the vertebrate skeleton evolved initially as a structure made of unmineralized cartilage. Steps toward a bony skeleton began 470 million years ago, with the appearance of mineralized bone on the outer surface of the skull in some jawless vertebrates. Shortly after that time, the internal skeleton began to mineralize, first as calcified cartilage. By 430 million years ago, some vertebrates had a thin layer of bone lining the cartilage of their internal skeleton. The bones of vertebrates underwent even more mineralization in the group we turn to next, the jawed vertebrates.

▼ Figure 34.12 Jawless armored vertebrates. *Pteraspis* and *Pharyngolepis* were two of many genera of jawless vertebrates that emerged during the Ordovician, Silurian, and Devonian periods.



CONCEPT CHECK 34.2

1. How are differences in the anatomy of lampreys and conodonts reflected in each animal's feeding method?
2. **WHAT IF?** In several different animal lineages, organisms with a head first appeared around 530 million years ago. Does this finding constitute proof that having a head is favored by natural selection? Explain.
3. **WHAT IF?** Suggest key roles that mineralized bone might have played in early vertebrates.

For suggested answers, see Appendix A.

CONCEPT 34.3

Gnathostomes are vertebrates that have jaws

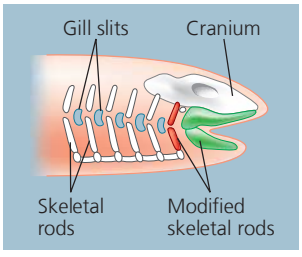
Hagfishes and lampreys are survivors from the early Paleozoic era, when jawless vertebrates were common. Since then, jawless vertebrates have been far outnumbered by the jawed vertebrates, the **gnathostomes**. Living gnathostomes are a diverse group that includes sharks and their relatives, ray-finned fishes, lobe-finned fishes, amphibians, reptiles (including birds), and mammals.

Derived Characters of Gnathostomes

Gnathostomes ("jaw mouth") are named for their jaws, hinged structures that, especially with the help of teeth, enable gnathostomes to grip food items firmly and slice them. According to one hypothesis, gnathostome jaws evolved by modification of the skeletal rods that had previously supported the anterior pharyngeal (gill) slits. **Figure 34.13** shows a stage in this evolutionary process in which several of these skeletal rods have been modified into precursors of jaws (green) and their structural supports (red). The remaining gill slits, no longer required for suspension feeding, remained as the major sites of respiratory gas exchange with the external environment.

Gnathostomes share other derived characters besides jaws. The common ancestors of all gnathostomes underwent an additional duplication of *Hox* genes, such that the single set present in early chordates became four. In fact, the entire genome appears to have duplicated, and together these genetic changes likely enabled the origin of jaws and other novel features in gnathostomes. The gnathostome forebrain is enlarged compared to that of other vertebrates, and it is associated with enhanced senses of smell and vision. Another characteristic of aquatic gnathostomes is the

▼ Figure 34.13 Possible step in the evolution of jawbones.



lateral line system, organs that form a row along each side of the body and are sensitive to vibrations in the surrounding water. Precursors of these organs were present in the head shields of some jawless vertebrates.

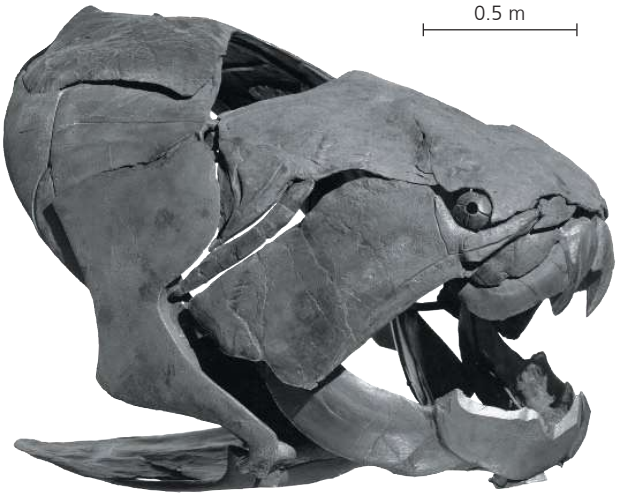
Fossil Gnathostomes

Gnathostomes appeared in the fossil record about 440 million years ago and steadily became more diverse. Their success probably resulted from a combination of anatomical features: Their paired fins and tail (which were also found in jawless vertebrates) allowed them to swim efficiently after prey, and their jaws enabled them to grab prey or simply bite off chunks of flesh. Over time, dorsal, ventral, and anal fins stiffened by bony structures called fin rays also evolved in some early gnathostomes. Fin rays provide thrust and steering control when aquatic vertebrates swim after prey or away from predators. Faster swimming was supported by other adaptations, including a more efficient gas exchange system in the gills.

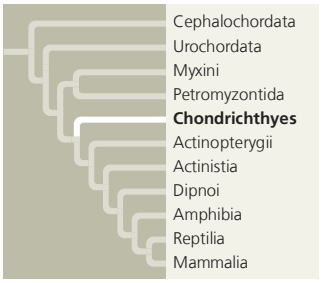
The earliest gnathostomes include extinct lineages of armored vertebrates known collectively as **placoderms**, which means "plate-skinned." Most placoderms were less than a meter long, though some giants measured more than 10 m **(Figure 34.14)**. Other jawed vertebrates, called **acanthodians**, emerged at roughly the same time and radiated during the Silurian and Devonian periods (444–359 million years ago). Placoderms had disappeared by 359 million years ago, and acanthodians became extinct about 70 million years later.

Overall, a series of recent fossil discoveries have revealed that 440–420 million years ago was a period of tumultuous evolutionary change. Gnathostomes that lived during this period had highly variable forms, and by 420 million years ago, they had diverged into the three lineages of jawed vertebrates that survive today: chondrichthyans, ray-finned fishes, and lobe-fins.

▼ Figure 34.14 Fossil of an early gnathostome. A formidable predator, the placoderm *Dunkleosteus* grew up to 10 m in length. Its jaw structure indicates that *Dunkleosteus* could exert a force of 560 kg/cm^2 (8,000 pounds per square inch) at the tip of its jaws.



Chondrichthyans (Sharks, Rays, and Their Relatives)



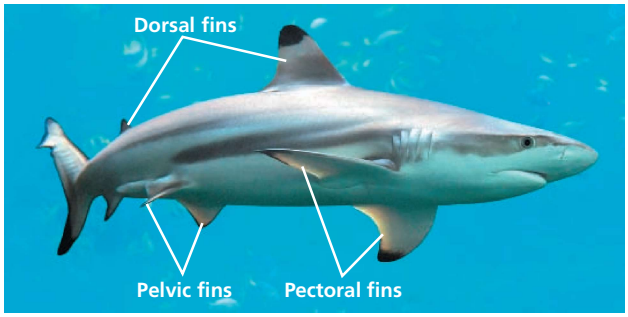
Sharks, rays, and their relatives include some of the biggest and most successful vertebrate predators in the oceans. They belong to the clade Chondrichthyes, which means "cartilage fish." As their name indicates, the **chondrichthyans** have a skeleton composed predominantly of cartilage, though often impregnated with calcium.

When the name Chondrichthyes was first coined, in the 1800s, scientists thought that chondrichthyans represented an early stage in the evolution of the vertebrate skeleton and that mineralization had evolved only in more derived lineages (such as "bony fishes"). However, as armored jawless vertebrates demonstrate, the mineralization of the vertebrate skeleton had already begun before the chondrichthyan lineage branched off from other vertebrates. Moreover, bone-like tissues have been found in early chondrichthyans, such as the fin skeleton of a shark that lived in the Carboniferous period. Traces of bone can also be found in living chondrichthyans—in their scales, at the base of their teeth, and, in some sharks, in a thin layer on the surface of their vertebrae. Such findings indicate that the restricted distribution of bone in the chondrichthyan body is a derived condition, emerging after chondrichthyans diverged from other gnathostomes.

There are about 1,000 species of living chondrichthyans. The largest and most diverse group consists of the sharks, rays, and skates **(Figure 34.15a** and **b)**. A second group is composed of a few dozen species of ratfishes, also called chimaeras **(Figure 34.15c)**.

Most sharks have a streamlined body and are swift swimmers, but they do not maneuver very well. Powerful movements of the trunk and the tail fin propel them forward. The dorsal fins function mainly as stabilizers, and the paired pectoral (fore) and pelvic (hind) fins are important for maneuvering. Although a shark gains buoyancy by storing a large amount of oil in its huge liver, the animal is still more dense than water, and if it stops swimming it sinks. Continual swimming also ensures that water flows into the shark's mouth and out through the gills, where gas exchange occurs. However, some sharks and many skates and rays spend a good deal of time resting on the seafloor. When resting, they use muscles of their jaws and pharynx to pump water over the gills.

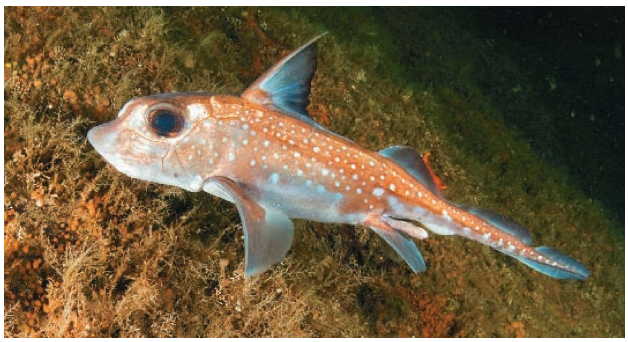
▼ **Figure 34.15 Chondrichthyans.**



(a) Blacktip reef shark (*Carcharhinus melanopterus*). Sharks are fast swimmers with acute senses. Like all gnathostomes, they have paired pectoral and pelvic fins.



(b) Southern stingray (*Dasyatis americana*). Most rays are bottom-dwellers that feed on molluscs and crustaceans. Some rays cruise in open water and scoop food into their gaping mouths.



(c) Spotted ratfish (*Hydrolagus colliei*). Ratfishes, or chimaeras, typically live at depths greater than 80 m and feed on shrimp, molluscs, and sea urchins. Some species have a venomous spine at the front of their first dorsal fin.

The largest sharks and rays are suspension feeders that consume plankton. Most sharks, however, are carnivores that swallow their prey whole or use their powerful jaws and sharp teeth to tear flesh from animals too large to swallow in one piece. Sharks have several rows of teeth that gradually move to the front of the mouth as old teeth are lost. The digestive tract of many sharks is proportionately shorter than that of many other vertebrates. Within the shark intestine is a *spiral valve*, a corkscrew-shaped ridge that increases surface area and prolongs the passage of food through the digestive tract.

Acute senses are adaptations that go along with the active, carnivorous lifestyle of sharks. Sharks have sharp vision but cannot distinguish colors. The nostrils of sharks, like those of most aquatic vertebrates, open into dead-end cups. They function only for olfaction (smelling), not for breathing. Like some other vertebrates, sharks have a pair of regions in the skin of their head that can detect electric fields generated by the muscle contractions of nearby animals. Like all nonmammalian aquatic vertebrates, sharks have no eardrums, structures that terrestrial vertebrates use to transmit sound waves in air to the auditory organs. Sound reaches a shark through water, and the animal's entire body transmits the sound to the hearing organs of the inner ear.

Shark eggs are fertilized internally. The male has a pair of claspers on its pelvic fins that transfer sperm into the female's reproductive tract. Some species of sharks are **oviparous**; they lay eggs that hatch outside the mother's body. These sharks release their fertilized eggs after encasing them in protective coats. Other species are **ovoviviparous**; they retain the fertilized eggs in the oviduct. Nourished by the egg yolk, the embryos develop into young that are born after hatching within the uterus. A few species are **viviparous**; the young develop within the uterus and obtain nourishment prior to birth by receiving nutrients from the mother's blood through a yolk sac placenta, by absorbing a nutritious fluid produced by the uterus, or by eating other eggs. The reproductive tract of the shark empties along with the excretory system and digestive tract into the **cloaca**, a common chamber that has a single opening to the outside.

Although rays are closely related to sharks, they have adopted a very different lifestyle. Most rays are bottom-dwellers that feed by using their jaws to crush molluscs and crustaceans. They have a flattened shape and use their greatly enlarged pectoral fins like water wings to propel themselves through the water. The tail of many rays is whiplike and, in some species, bears venomous barbs that function in defense.

Chondrichthyans have thrived for over 400 million years. Today, however, they are severely threatened by overfishing. For example, a recent report indicated that shark populations in the Pacific have plummeted by up to 95%, and shark populations that live closest to people have declined the most.

Ray-Finned Fishes and Lobe-Fins



The vast majority of vertebrates belong to the clade of gnathostomes called Osteichthyes. Unlike chondrichthyans, nearly all living **osteichthyans** have an ossified (bony) endoskeleton with a hard matrix of calcium phosphate. The name Osteichthyes ("bony fish") was coined long before the advent of phylogenetic systematics. When it was originally defined, the group excluded tetrapods, but we now know that such a taxon would be paraphyletic (see Figure 34.2). Therefore, systematists today include tetrapods along with bony fishes in the clade Osteichthyes. Clearly, the name of the group does not accurately describe all of its members.

This section discusses the aquatic osteichthyans known informally as fishes. Most fishes breathe by drawing water over four or five pairs of gills located in chambers covered by a protective bony flap called the **operculum** (Figure 34.16). Water is drawn into the mouth, through the pharynx, and out between the gills by movement of the operculum and contraction of muscles surrounding the gill chambers.

Most fishes can maintain a buoyancy equal to the surrounding water by filling an air sac known as a **swim bladder**. (If a fish swims to greater depths or toward the surface, where water pressure differs, the fish shuttles gas between its blood and swim bladder, keeping the volume of gas in the bladder constant.) Charles Darwin proposed that the lungs of tetrapods evolved from swim bladders, but strange as it may sound, the opposite seems to be true: Swim bladders arose from lungs. Osteichthyans in many early-branching lineages have lungs, which they use to breathe air as a supplement to gas exchange in their gills. This suggests that lungs arose in early osteichthyans; later, swim bladders evolved from lungs in some lineages.

In nearly all fishes, the skin is covered by flattened, bony scales that differ in structure from the tooth-like scales of sharks. Glands in the skin secrete a slimy mucus over the skin, an adaptation that reduces drag during swimming. Like the ancient aquatic gnathostomes mentioned earlier, fishes have a lateral line system, which is evident as a row of tiny pits in the skin on either side of the body.

The details of fish reproduction vary extensively. Most species are oviparous, reproducing by external fertilization after the female sheds large numbers of small eggs. However, internal fertilization and birthing characterize other species.

Ray-Finned Fishes

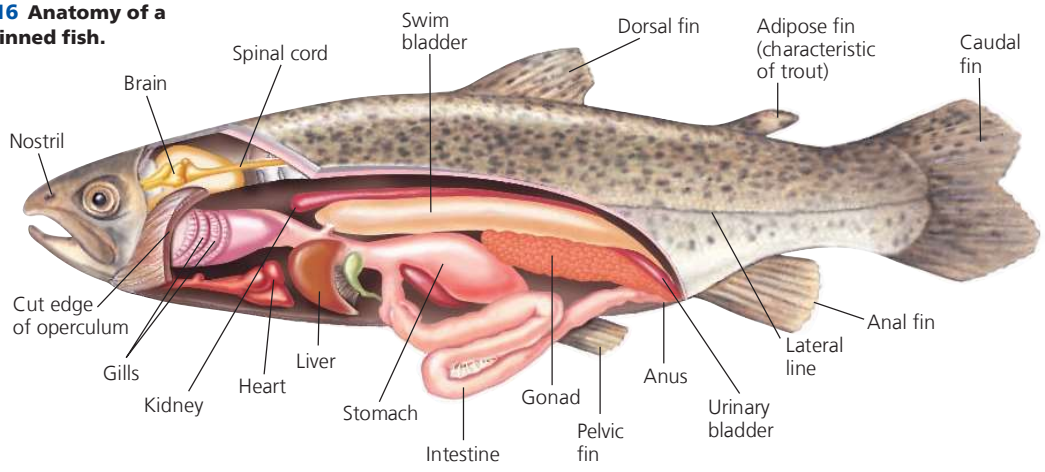
Nearly all the aquatic osteichthyans familiar to us are among the over 27,000 species of **ray-finned fishes** (Actinopterygii) (Figure 34.17). Named for the bony rays that support their fins, the ray-finned fishes originated during the Silurian period (444–419 million years ago). The group has diversified greatly since that time, resulting in numerous species and many modifications in body form and fin structure that affect maneuvering, defense, and other functions.

Ray-finned fishes serve as a major source of protein for humans, who have harvested them for thousands of years. However, industrial-scale fishing operations have driven some of the world's biggest fisheries to collapse. For example, after decades of abundant harvests, in the 1990s the catch of cod (*Gadus morhua*) in the northwest Atlantic plummeted to just 5% of its historic maximum, bringing cod fishing there to a near halt. Despite ongoing restrictions on the fishery, cod populations have yet to recover to sustainable levels. Ray-finned fishes also face other pressures from humans, such as the diversion of rivers by dams. Changing water flow patterns can hamper the fishes' ability to obtain food and interferes with migratory pathways and spawning grounds.

Lobe-Fins

Like the ray-finned fishes, the other major lineage of osteichthyans, the **lobe-fins** (Sarcopterygii), also originated during

▼ Figure 34.16 Anatomy of a trout, a ray-finned fish.





▲ Yellowfin tuna (*Thunnus albacares*) is a fast-swimming schooling fish that is commercially important worldwide.



▶ Native to coral reefs of the Pacific Ocean, the brightly colored red lionfish (*Pterois volitans*) can inject venom through its spines, causing a severe and painful reaction in humans.



▲ The sea horse has a highly modified body form, as exemplified by *Hippocampus ramulosus,* shown above. Sea horses are unusual among animals in that the male carries the young during their embryonic development.



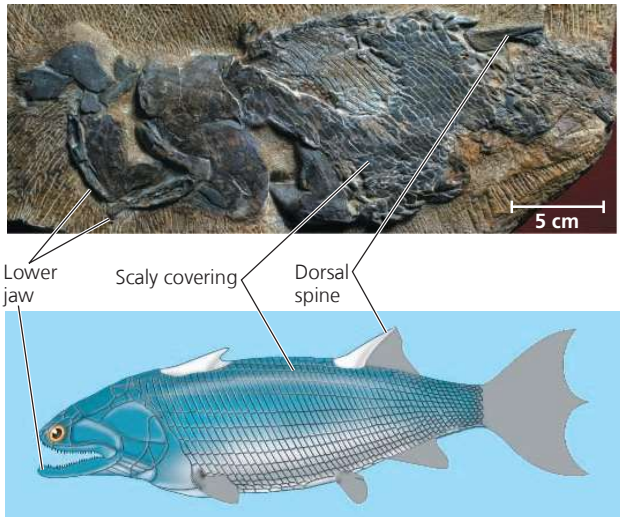
▲ The fine-spotted moray eel (*Gymnothorax dovii*) is a predator that ambushes prey from crevices in its coral reef habitat.

▲ Figure 34.17 Ray-finned fishes (Actinopterygii).

Mastering Biology Video: Sea Horse Camouflage

the Silurian period **(Figure 34.18)**. The key derived character of lobe-fins is the presence of rod-shaped bones surrounded by a thick layer of muscle in their pectoral and pelvic fins. During the Devonian (419–359 million years ago), many lobe-fins lived in brackish waters, such as in coastal wetlands. There they may have used their lobed fins to help them move across logs or the muddy bottom (as do some living lobe-fins). Some Devonian lobe-fins were gigantic predators. It is not uncommon to find spike-shaped fossils of Devonian lobe-fin teeth as big as your thumb.

By the end of the Devonian period, lobe-fin diversity was dwindling, and today only three lineages survive. One lineage,

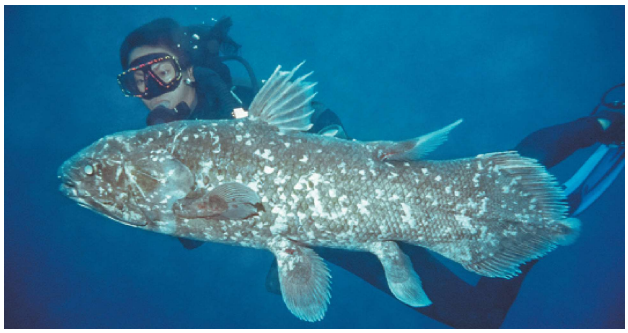


▲ Figure 34.18 A reconstruction of an ancient lobe-fin. Discovered in 2009, *Guiyu oneiros* is the earliest known lobe-fin, dating to 420 million years ago. The fossil of this species was nearly complete, allowing for an accurate reconstruction; regions shown in gray were missing from the fossil.

the coelacanths (Actinistia), was thought to have become extinct 75 million years ago. However, in 1938, fishermen caught a living coelacanth off the east coast of South Africa **(Figure 34.19)**. Until the 1990s, all subsequent discoveries were near the Comoros Islands in the western Indian Ocean. Since 1999, coelacanths have also been found at various places along the eastern coast of Africa and in the eastern Indian Ocean, near Indonesia. The Indonesian population may represent a second species.

The second lineage of living lobe-fins, the lungfishes (Dipnoi), is represented today by six species in three genera, all of which are found in the Southern Hemisphere. Lungfishes arose in the ocean but today are found only in fresh water, generally in stagnant ponds and swamps. They surface to gulp air into lungs connected to their pharynx. Lungfishes also have gills, which are the main organs for gas exchange in Australian lungfishes. When ponds shrink during the dry season, some lungfishes can burrow into the mud and estivate (wait in a state of torpor; see Concept 40.4).

▼ Figure 34.19 A coelacanth *(Latimeria)*. These lobe-fins were found living off the coasts of southern Africa and Indonesia.



The third lineage of lobe-fins that survives today is far more diverse than the coelacanths or the lungfishes. During the mid-Devonian, these organisms adapted to life on land and gave rise to vertebrates with limbs and feet, called tetrapods—a lineage that includes humans.

CONCEPT CHECK 34.3

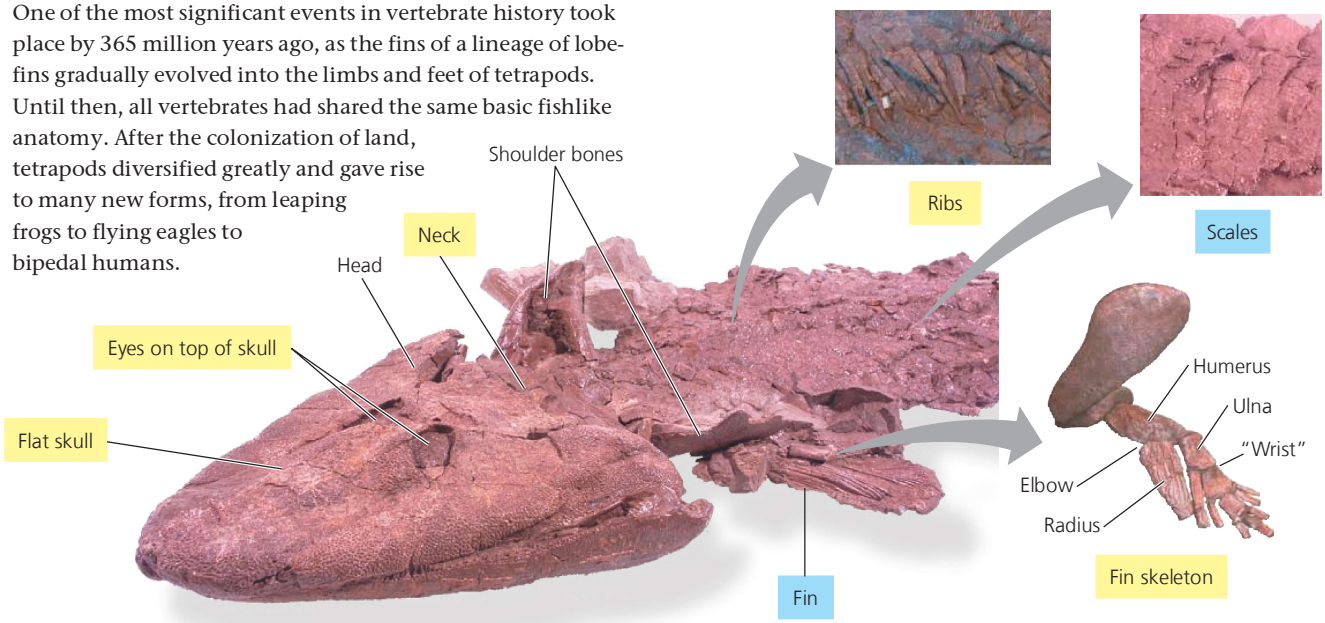
1. What derived characters do sharks and tuna share? What features distinguish tuna from sharks?
2. Describe key adaptations of aquatic gnathostomes.
3. **DRAW IT** Redraw Figure 34.2 to show four lineages: cyclostomes, lancelets, gnathostomes, and tunicates. Label the vertebrate common ancestor and circle the lineage that includes humans.
4. **WHAT IF?** Imagine that we could replay the history of life. Is it possible that a group of vertebrates that colonized land could have arisen from aquatic gnathostomes other than the lobe-fins? Explain.

For suggested answers, see Appendix A.

CONCEPT 34.4

Tetrapods are gnathostomes that have limbs

One of the most significant events in vertebrate history took place by 365 million years ago, as the fins of a lineage of lobe-fins gradually evolved into the limbs and feet of tetrapods. Until then, all vertebrates had shared the same basic fishlike anatomy. After the colonization of land, tetrapods diversified greatly and gave rise to many new forms, from leaping frogs to flying eagles to bipedal humans.



Fish Characters	Tetrapod Characters
Scales	Neck
Fins	Ribs
Gills and lungs	Fin skeleton
	Flat skull
	Eyes on top of skull

▲ **Figure 34.20 Discovery of a "fishapod": *Tiktaalik*.** Paleontologists were on the hunt for fossils that could shed light on the evolutionary origin of tetrapods. Based on the ages of previously discovered fossils, researchers were looking for a dig site with rocks about 365–385 million years old. Ellesmere Island, in the Canadian Arctic, was one of the few such sites that was also likely to contain fossils, because it was once a river. The search at this site was rewarded by the discovery of fossils of a 375-million-year-old lobe-fin, named *Tiktaalik*. As shown in the chart and photographs, *Tiktaalik* exhibits both fish and tetrapod characters.

MAKE CONNECTIONS *Describe how* Tiktaalik's *features illustrate Darwin's concept of descent with modification (see Concept 22.2).*

Mastering Biology HHMI Video: Great Transitions: The Origin of Tetrapods

Derived Characters of Tetrapods

The most significant character of **tetrapods** gives the group its name, which means "four feet" in Greek. In place of pectoral and pelvic fins, tetrapods have limbs with digits. Limbs support a tetrapod's weight on land, while feet with digits efficiently transmit muscle-generated forces to the ground when it walks.

Life on land selected for numerous other changes to the tetrapod body plan. In tetrapods, the head is separated from the body by a neck that originally had one vertebra on which the skull could move up and down. Later, with the origin of a second vertebra in the neck, the head could also swing from side to side. The bones of the pelvic girdle, to which the hind legs are attached, are fused to the backbone, permitting forces generated by the hind legs against the ground to be transferred to the rest of the body. Except for some fully aquatic species (such as the axolotl; see Figure 42.1), the adults of living tetrapods do not have gills; during embryonic development, the pharyngeal clefts instead give rise to parts of the ears, certain glands, and other structures.

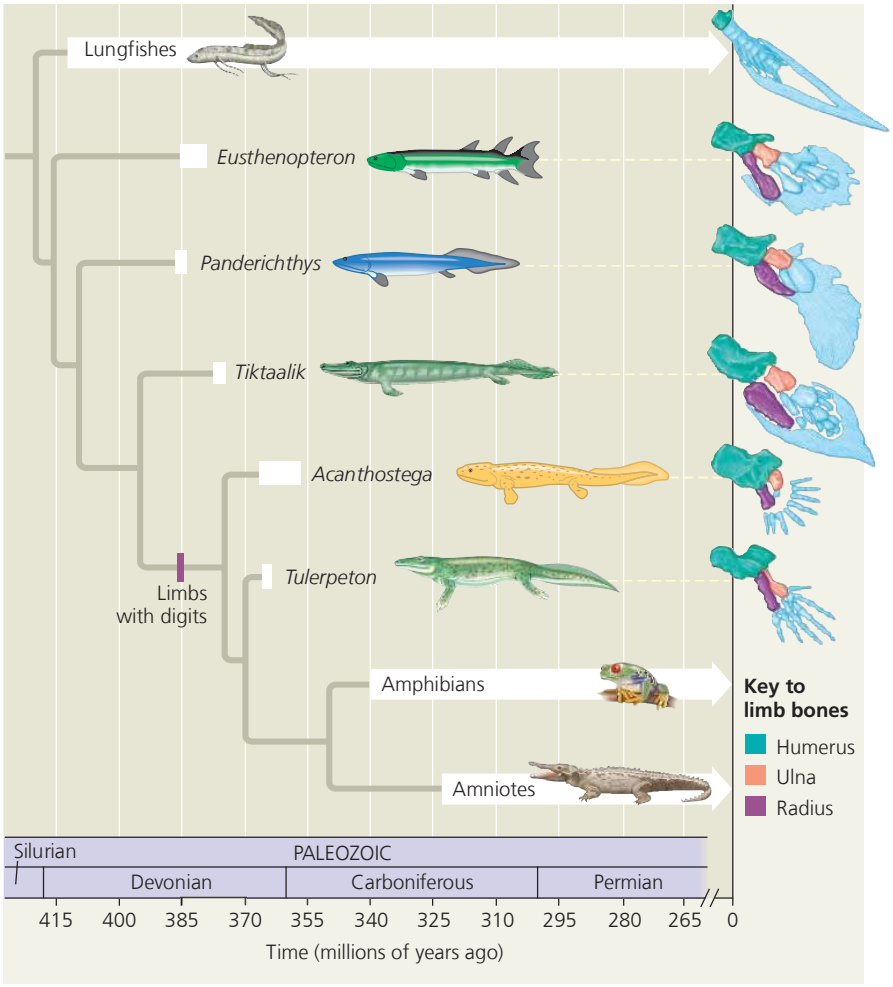
We'll discuss later how some of these characters were dramatically altered or lost in various lineages of tetrapods. In birds, for example, the pectoral limbs became wings, and in whales, the entire body converged toward a fishlike shape.

The Origin of Tetrapods

As you have read, the Devonian coastal wetlands were home to a wide range of lobe-fins. Those that entered shallow, oxygen-poor water could have used their lungs to breathe air. Some species probably used their stout fins to swim and "walk" underwater across the bottom (moving their fins in an alternating gait, as do some living lobe-fins). This suggests that the tetrapod body plan did not evolve "out of nowhere" but was simply a modification of a preexisting body plan.

The recent discovery of a fossil called *Tiktaalik* provided new details on how this process of modification occurred **(Figure 34.20)**. Like a fish, this species had fins, gills, and lungs, and its body was covered in scales. But unlike a fish, *Tiktaalik* had a full set of ribs that would have helped it breathe air and support its body. Also unlike a fish, *Tiktaalik* had a neck, allowing it to move its head about. In addition, the bones of *Tiktaalik*'s front fin have the same basic pattern found in all limbed animals: one bone (the humerus), followed by two bones (the radius and ulna), followed by a group of small bones that comprise the wrist. Finally, *Tiktaalik*'s pelvis and rear fin were larger and more robust than those of a fish; the pelvis is the bony structure to which hind limbs are attached in tetrapods. Although it is unlikely that *Tiktaalik* could walk on land, the skeletal structure of its fins and pelvis suggests that it could prop itself up and walk in water on its fins. Since *Tiktaalik* predates the oldest known tetrapod, its features suggest that key "tetrapod" traits, such as a wrist, ribs, and a neck, were in fact ancestral to the tetrapod lineage.

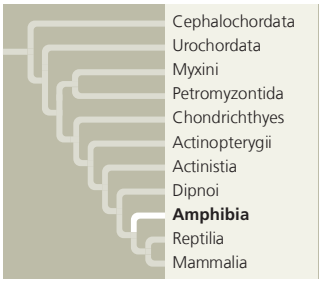
Tiktaalik and other extraordinary fossil discoveries have allowed paleontologists to reconstruct how fins became progressively more limb-like over time, culminating in the appearance in the fossil record of the first tetrapods 365 million years ago **(Figure 34.21)**. Over the next 60 million years, a great diversity of tetrapods arose. Some of these species retained functional gills and had weak limbs, while others lost their gills and had stronger limbs that facilitated walking on land. Overall, judging from the morphology and locations of their fossils, most of these early tetrapods probably remained tied to water, a characteristic they share with some members of the most basal group of living tetrapods, the amphibians.



▲ **Figure 34.21 Steps in the origin of limbs with digits.** The white bars on the branches of this diagram place known fossils in time; arrowheads indicate lineages that extend to today. The drawings of extinct organisms are based on fossilized skeletons, but the colors are fanciful.

VISUAL SKILLS *Assuming the branch point dates shown in this diagram are accurate, what range of dates would include the origin of amphibians?*

Amphibians



The **amphibians** are represented today by about 6,150 species in three clades: salamanders (clade Urodela, "tailed ones"), frogs (clade Anura, "tailless ones"), and caecilians (clade Apoda, "legless ones").

Salamanders

There are about 550 known species of urodeles, or salamanders. Some are entirely aquatic, but others live on land as adults or throughout life. Most salamanders that live on land walk with a side-to-side bending of the body, a trait



(a) Order Urodela. Urodeles (salamanders) retain their tail as adults.



(b) Order Anura. Anurans (toads and frogs) lack a tail as adults.



(c) Order Apoda. Apodans, or caecilians, are legless, mainly burrowing amphibians.

▲ Figure 34.22 Amphibians.

also found in early terrestrial tetrapods **(Figure 34.22a)**. Paedomorphosis is common among aquatic salamanders; the axolotl, for instance, retains larval features even when sexually mature (see Figure 25.25).

Frogs

Numbering about 5,420 species, anurans, or frogs, are better suited than salamanders to locomotion on land **(Figure 34.22b)**. Adult frogs use their powerful hind legs to hop along the terrain. Although often distinctive in appearance, the animals known as "toads" are simply frogs that have leathery skin or other adaptations for life on land. A frog nabs insects and other prey by flicking out its long, sticky tongue, which is attached to the front of the mouth. Frogs display a great variety of adaptations that help them avoid being eaten by larger predators. Their skin glands secrete distasteful or even poisonous mucus. Many poisonous species have color patterns that camouflage them or have bright coloration, which predators appear to associate with danger (see Figure 54.6).

Caecilians

The approximately 170 species of apodans, or caecilians, are legless and nearly blind, and superficially they resemble earthworms **(Figure 34.22c)**. Their absence of legs is a secondary adaptation, as they evolved from a legged ancestor. Caecilians inhabit tropical areas, where most species burrow in moist forest soil.



(a) The tadpole is an aquatic herbivore with a fishlike tail and internal gills.



(b) During metamorphosis, the gills and tail are resorbed, and walking legs develop. The adult frog will live on land.



(c) The adults return to water to mate. The male grasps the female, stimulating her to release eggs. The eggs are laid and fertilized in water. They have a jelly coat but lack a shell and would desiccate in air.

▲ Figure 34.23 The "dual life" of a frog (*Rana temporaria*).

Lifestyle and Ecology of Amphibians

The term *amphibian* (derived from *amphibious*, meaning "both ways of life") refers to the life stages of many frog species that live first in water and then on land **(Figure 34.23)**. The larval stage of a frog, called a tadpole, is usually an aquatic herbivore with gills, a lateral line system resembling that of aquatic vertebrates, and a long, finned tail. The tadpole initially lacks legs; it swims by undulating its tail. During the metamorphosis that leads to the "second life," the tadpole develops legs, lungs, a pair of external eardrums, and a digestive system adapted to a carnivorous diet. At the same time, the gills disappear; the lateral line system also disappears in most species. The young frog crawls onto shore and becomes a terrestrial hunter. In spite of their name, however, many amphibians do not live a dual—aquatic and terrestrial—life. There are some strictly aquatic or strictly terrestrial frogs, salamanders, and caecilians. Moreover, salamander and caecilian larvae look much like the adults, and typically both the larvae and the adults are carnivorous.

Most amphibians are found in damp habitats such as swamps and rain forests. Even those adapted to drier habitats spend much of their time in burrows or under moist leaves, where humidity is high. One reason amphibians require relatively wet habitats is that they rely heavily on their moist skin for gas exchange—if their skin dries out, they cannot get enough oxygen. In addition, amphibians typically lay their eggs in water or in moist environments on land; their eggs lack a shell and dehydrate quickly in dry air.

Fertilization is external in most amphibians; the male grasps the female and spills his sperm over the eggs as the female sheds them (see Figure 34.23c). Some amphibian species lay vast numbers of eggs in temporary pools, and egg mortality is high. In contrast, other species lay relatively few



◀ Figure 34.24 A mobile nursery. A female marsupial frog (*Flectonotus fitzgeraldi*) incubates her eggs in pouches of skin on her back.

eggs and display various types of parental care. Depending on the species, either males or females may house eggs on their back **(Figure 34.24)**, in their mouth, or even in their stomach. Certain tropical tree frogs stir their egg masses into moist, foamy nests that resist drying.

Many amphibians exhibit complex and diverse social behaviors, especially during breeding seasons. Frogs are usually quiet, but the males of many species vocalize to defend their breeding territory or to attract females. In some species, migrations to specific breeding sites may involve vocal communication, celestial navigation, or chemical signaling.

Over the past 30 years, zoologists have documented a rapid and alarming decline in amphibian populations in locations throughout the world. There appear to be several causes, including the spread of a disease-causing chytrid fungus (see Figure 31.25), habitat loss, climate change, and pollution. In some cases, declines have become extinctions. Recent studies indicate that at least nine amphibian species have become extinct within the last four decades; more than 100 other species have not been observed in that time and are considered possibly extinct. In the **Problem-Solving Exercise**, you can explore one possible strategy to prevent amphibian deaths from fungal infections.

PROBLEM-SOLVING EXERCISE

Can declining amphibian populations be saved by a vaccine?

Amphibian populations are declining rapidly worldwide. The fungus *Batrachochytrium dendrobatidis* (*Bd*) has contributed to this decline: This pathogen causes severe skin infections in many amphibian species, leading to massive die-offs. Efforts to save amphibians from *Bd* have had limited success, and there is little evidence that frogs and other amphibians have acquired resistance to *Bd* on their own.

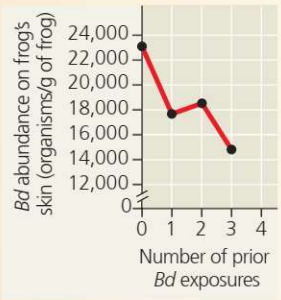


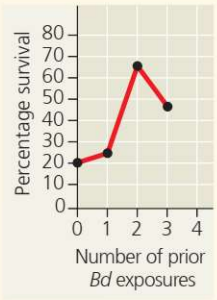
Yellow-legged frogs (*Rana muscosa*) in California killed by *Bd* infection

In this exercise, you will investigate whether amphibians can acquire resistance to the fungal pathogen *Bd*.

Your Approach The principle guiding your investigation is that prior exposure to a pathogen can enable amphibians to acquire immunological resistance to that pathogen. To see whether this occurs after exposure to *Bd*, you will analyze data on acquired resistance in Cuban tree frogs (*Osteopilus septentrionalis*).

Your Data To create variation in number of prior exposures to *Bd*, Cuban tree frogs were exposed to *Bd* and cleared of their infection (using heat treatments) from zero to three times; frogs with no prior exposures are referred to as "naive." Researchers then exposed frogs to *Bd* and measured mean abundance of *Bd* on the frog's skin, frog survival, and abundance of lymphocytes (a type of white blood cell involved in the vertebrate immune response).





Number of prior *Bd* exposures	Thousands of lymphocytes per g of frog
0	134
1	240
2	244
3	227

Your Analysis

1. Describe and interpret the results shown in the figure.
2. **(a)** Graph the data in the table. **(b)** Based on these data, develop a hypothesis that explains the results discussed in question 1.
3. Breeding populations of amphibian species threatened by *Bd* have been established in captivity. In addition, evidence suggests that Cuban tree frogs can acquire resistance after exposure to dead *Bd*. Based on this information and your answers to questions 1 and 2, suggest a strategy for repopulating regions decimated by *Bd*.

Instructors: A version of this Problem-Solving Exercise can be assigned in **Mastering Biology**.

CONCEPT CHECK 34.4

1. Describe the origin of tetrapods and identify some of their key derived traits.
2. Some amphibians never leave the water, whereas others can survive in relatively dry terrestrial environments. Contrast the adaptations that facilitate these two lifestyles.
3. **WHAT IF?** Scientists think that amphibian populations may provide an early warning system of environmental problems. What features of amphibians might make them particularly sensitive to environmental problems?

For suggested answers, see Appendix A.

CONCEPT 34.5

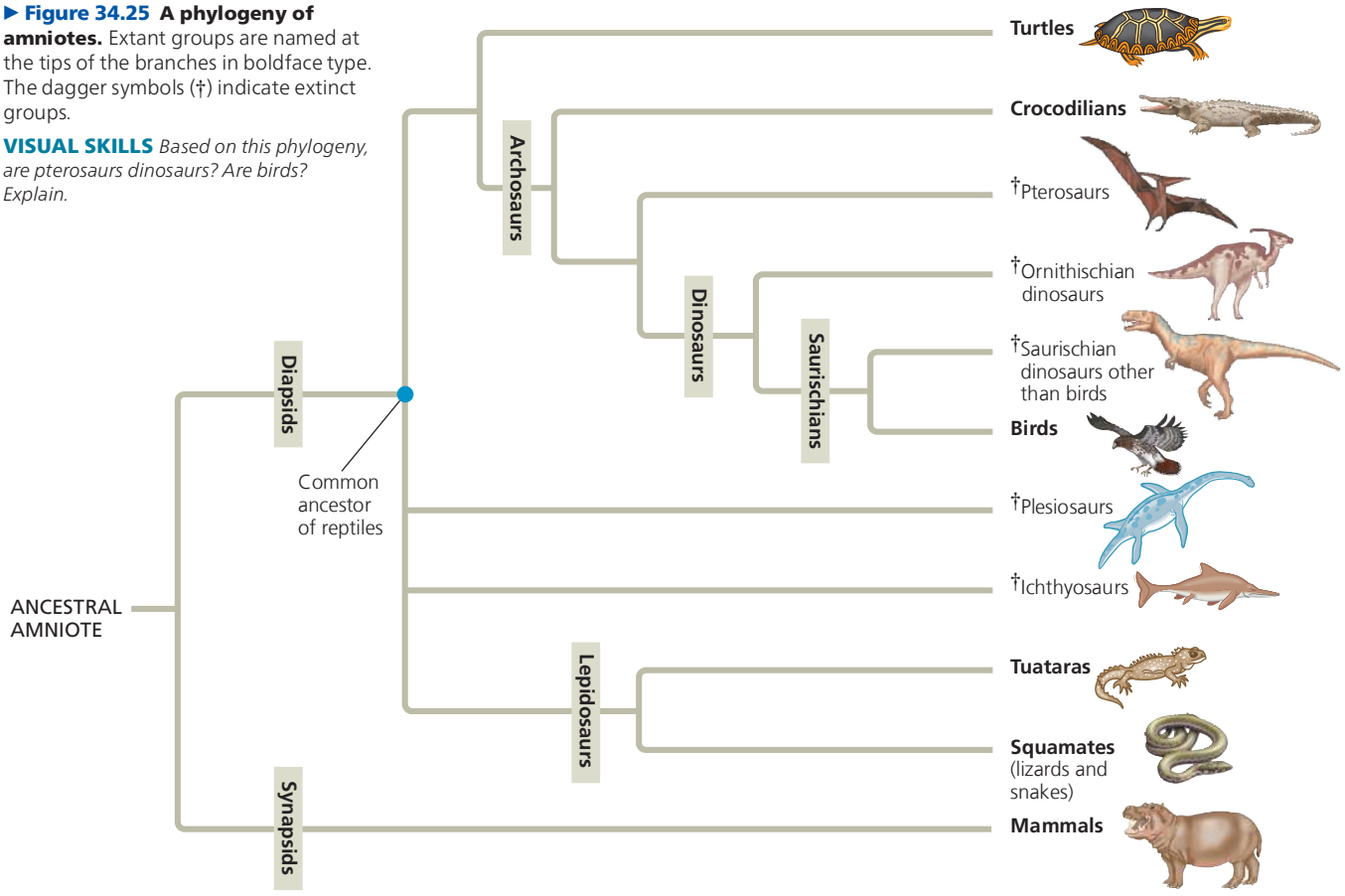
Amniotes are tetrapods that have a terrestrially adapted egg

The **amniotes** are a group of tetrapods whose extant members are the reptiles (including birds, as we'll discuss in this section) and mammals **(Figure 34.25)**. During their evolution, amniotes acquired a number of new adaptations to life on land.

Derived Characters of Amniotes

Amniotes are named for the major derived character of the clade, the **amniotic egg**, which contains four specialized membranes: the amnion, the chorion, the yolk sac, and the allantois **(Figure 34.26)**. Called *extraembryonic membranes* because they are not part of the body of the embryo itself, these membranes develop from tissue layers that grow out from the embryo. The amniotic egg is named for the amnion, which encloses a compartment of fluid that bathes the embryo and acts as a hydraulic shock absorber. The other membranes in the egg function in gas exchange, the transfer of stored nutrients to the embryo, and waste storage. The amniotic egg was a key evolutionary innovation for terrestrial life: It allowed the embryo to develop on land in its own private "pond," hence reducing the dependence of tetrapods on an aqueous environment for reproduction.

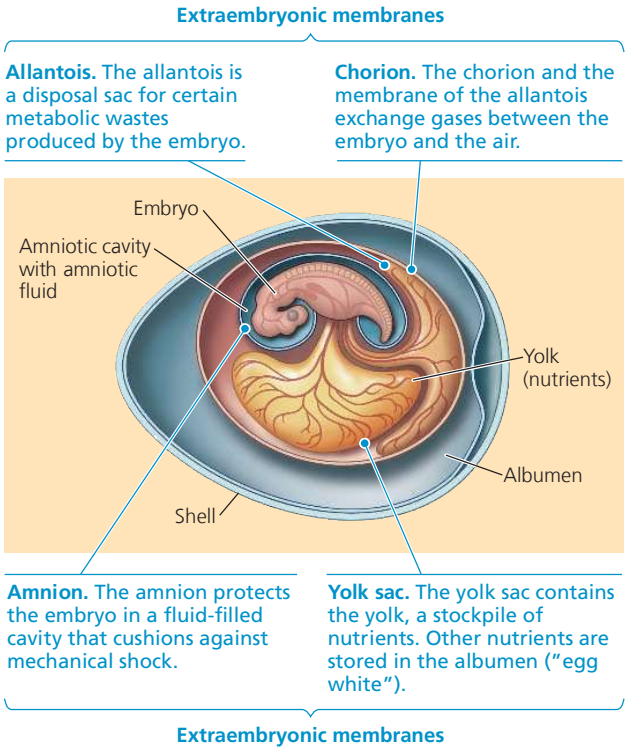
In contrast to the shell-less eggs of amphibians, the amniotic eggs of most reptiles and some mammals have a shell. A shell slows dehydration of the egg in air, an adaptation that helped amniotes to occupy a wider range of terrestrial habitats than amphibians, their closest living relatives. (Seeds played a similar role in the evolution of plants, as discussed in Concept 30.1.)



▶ Figure 34.25 A phylogeny of amniotes. Extant groups are named at the tips of the branches in boldface type. The dagger symbols (†) indicate extinct groups.

VISUAL SKILLS *Based on this phylogeny, are pterosaurs dinosaurs? Are birds? Explain.*

▼ Figure 34.26 The amniotic egg. The embryos of reptiles and mammals form four extraembryonic membranes: the allantois, chorion, amnion, and yolk sac. This diagram shows these membranes in the shelled egg of a reptile.



Most mammals have lost the eggshell over the course of their evolution, and the embryo avoids desiccation by developing within the amnion inside the mother's body.

Amniotes have acquired other key adaptations to life on land. For example, amniotes use their rib cage to ventilate their lungs. This method is more efficient than throat-based ventilation, which amphibians use as a supplement to breathing through their skin. The increased efficiency of rib cage ventilation may have allowed amniotes to abandon breathing through their skin and develop less permeable skin, thereby conserving water.

Early Amniotes

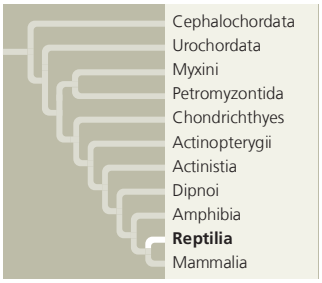
The most recent common ancestor of living amphibians and amniotes lived 350 million years ago. Based on where their fossils have been found, the earliest amniotes lived in warm, moist areas, as did the first tetrapods. Over time, early amniotes expanded into a wide range of new environments, including dry and high-latitude regions. Fossil evidence shows that the earliest amniotes resembled small lizards with sharp teeth, a sign that they were predators **(Figure 34.27)**. Later groups of amniotes also included herbivores, as evidenced by their grinding teeth and other features.

▼ Figure 34.27 Artist's reconstruction of *Hylonomus*, an early amniote. About 25 cm long, this species lived 310 million years ago and probably ate insects and other small invertebrates.



Present-day amniotes include two large clades of terrestrial vertebrates: reptiles and mammals.

Reptiles



Living members of the **reptile** clade include turtles, tuataras, lizards and snakes, crocodilians, and birds (see Figure 34.25). There are about 20,800 species of reptiles, the majority of which are squamates (lizards and snakes; 10,425 species) or birds (10,000 species).

As a group, the reptiles share several derived characters that distinguish them from other tetrapods. For example, unlike amphibians, reptiles have scales that contain the protein keratin (as does a human nail). Scales help protect the animal's skin from desiccation and abrasion. In addition, most reptiles lay their shelled eggs on land; the shell protects the egg from drying out **(Figure 34.28)**. Fertilization occurs internally, before the eggshell is secreted.

Reptiles such as lizards and snakes are sometimes described as "cold-blooded" because they do not use their metabolism

▼ Figure 34.28 Hatching reptiles. These baby panther chameleons (*Furcifer pardalis*) are breaking out of their parchment-like shells, a common type of shell among living reptiles other than birds.



extensively to control their body temperature. However, they do regulate their body temperature by using behavioral adaptations. For example, many lizards bask in the sun when the air is cool and seek shade when the air is too warm. A more accurate description of these reptiles is to say that they are **ectothermic**, which means that they absorb external heat as their main source of body heat. By warming themselves directly with solar energy rather than through the metabolic breakdown of food, an ectothermic reptile can survive on less than 10% of the food energy required by a mammal of the same size. But the reptile clade is not entirely ectothermic; birds are **endothermic**, capable of maintaining body temperature through metabolic activity.

The Origin and Evolutionary Radiation of Reptiles

Fossil evidence indicates that the earliest reptiles lived about 310 million years ago and resembled lizards. Like all reptiles today, these early reptiles were **diapsids**. A key derived character of diapsids is a pair of holes on each side of the skull, behind the eye sockets; muscles pass through these holes and attach to the jaw, controlling jaw movement.

The diapsids are composed of three main lineages. The first lineage includes the turtles. A second lineage gave rise to the **lepidosaurs**, which include tuataras, lizards, and snakes. This lineage also produced some marine reptiles, including the giant mososaurs. Some of these marine species rivaled today's whales in length; all of them are extinct. The third diapsid lineage, the **archosaurs**, produced the crocodilians, pterosaurs, and dinosaurs. Our focus here will be on extinct lineages of archosaurs; we'll discuss living reptiles shortly.

Pterosaurs, which originated in the late Triassic, were the first tetrapods to exhibit flapping flight. The pterosaur wing was completely different from the wings of birds and bats. It consisted of a collagen-strengthened membrane that stretched between the trunk or hind leg and a very long digit on the foreleg. The smallest pterosaurs were no bigger than a sparrow, and the largest had a wingspan of nearly 11 m. They appear to have converged on many of the ecological roles later played by birds; some were insect-eaters, others grabbed fish out of the ocean, and still others filtered small animals through thousands of fine needlelike teeth. But by 66 million years ago, pterosaurs had become extinct.

On land, the **dinosaurs** diversified into a vast range of shapes and sizes, from bipeds the size of a pigeon to 45-m-long quadrupeds with necks long enough to let them browse the tops of trees. One lineage of dinosaurs, the ornithischians, were herbivores; they included many species with elaborate defenses against predators, such as tail clubs and horned crests. The other main lineage of dinosaurs, the saurischians, included the long-necked giants and a group called the **theropods**, which were bipedal carnivores. Theropods included the famous *Tyrannosaurus rex* as well as the ancestors of birds.

Dinosaurs once were considered slow, sluggish creatures. Since the 1970s, however, fossil discoveries and research have led to the conclusion that many dinosaurs were agile and fast moving. Dinosaurs had a limb structure that enabled them to walk and run more efficiently than could earlier tetrapods, which had a sprawling gait. Fossilized footprints and other evidence suggest that some species were social—they lived and traveled in groups, much as many mammals do today. Paleontologists have also discovered evidence that some dinosaurs built nests and protected their eggs, as birds do today (see Figure 26.17). Finally, some anatomical evidence supports the hypothesis that at least some dinosaurs were endotherms.

All dinosaurs except birds became extinct by the end of the Cretaceous period (66 million years ago). Their extinction may have been caused at least in part by the asteroid or comet impact described in Concept 25.4. Some analyses of the fossil record are consistent with this idea in that they show a sudden decline in dinosaur diversity at the end of the Cretaceous. However, other analyses indicate that the number of dinosaur species had begun to decline several million years before the Cretaceous ended. Further fossil discoveries and new analyses will be needed to resolve this debate.

Next, we'll discuss the three extant lineages of reptiles, the turtles, lepidosaurs (tuataras, lizards, and snakes), and archosaurs (crocodilians and birds).



Mastering Biology
Interview with Paul Sereno: Adventures hunting dinosaurs

Mastering Biology HHMI Video: How to Find a Dinosaur

Turtles

Turtles are one of the most distinctive groups of reptiles alive today. For example, turtles do not have any holes in their skull behind the eye sockets, whereas other reptiles have two holes behind each eye socket. Recall that such skull holes are a key derived trait of the diapsids. Thus, until recently it was not clear whether turtles—like all other living reptiles—should be classified within the diapsid clade. However, in 2015, new fossil discoveries showed that early turtles had the skull openings found in other diapsids. This suggests that turtles are diapsids that have lost the holes in their skull over

▼ Figure 34.29 Extant reptiles (other than birds).

(a) Black-breasted hill turtle (*Geoemyda spengleri*)



the course of evolution. Moreover, recent phylogenomic studies indicate that turtles are nested within the diapsid clade and are more closely related to crocodilians and birds than to other reptiles (see Figure 34.25).

All turtles have a boxlike shell made of upper and lower shields that are fused to the vertebrae, clavicles (collarbones), and ribs **(Figure 34.29a)**. Most of the 351 known species of turtles have a hard shell, providing excellent defense against predators. Fossil evidence shows that *Pappochelys*, a turtle that lived 240 million years ago, had a series of hard, shell-like bones along its belly. By 220 million years ago, another early turtle had a complete lower shell but an incomplete upper shell, suggesting that turtles acquired full shells in stages.

The earliest turtles could not retract their head into their shell, but mechanisms for doing so evolved independently in two separate branches of turtles. The side-necked turtles fold their neck horizontally, while the vertical-necked turtles fold their neck vertically.

Some turtles have adapted to deserts, and others live almost entirely in ponds and rivers. Still others live in the sea. Sea turtles have a reduced shell and enlarged forelimbs that function as flippers. They include the largest living turtles, the deep-diving leatherbacks, which can exceed a mass of 1,500 kg and feed on jellies. Leatherbacks and other sea turtles are endangered by being caught in fishing nets, as well as by the residential and commercial development of the beaches where the turtles lay their eggs.

Lepidosaurs

One surviving lineage of lepidosaurs is represented by a single species, a lizard-like reptile called the tuatara **(Figure 34.29b)**. Fossil evidence indicates that tuatara ancestors lived at least 220 million years ago. These organisms thrived on many continents well into the Cretaceous period and reached up to a meter in length. Today, however, tuataras are found only on 30 islands off the coast of New Zealand. When humans arrived in New Zealand 750 years ago, the rats that accompanied them devoured tuatara eggs, eventually eliminating the reptiles on the main islands. The tuataras that remain on the outlying islands are about 50 cm long and feed on insects, small lizards, and bird eggs and chicks. They can live to be over 100 years old. Their future survival depends on whether their remaining habitats are kept rat-free.

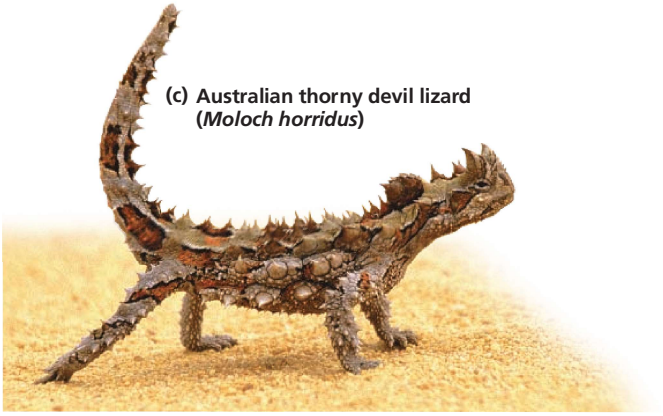
The other major living lineage of lepidosaurs consists of the lizards and snakes, or squamates, which number 10,425 species **(Figure 34.29c** and **d)**. Many squamates are small; the Jaragua lizard, discovered recently in the Dominican Republic, is only 16 mm long—small enough to fit comfortably on a dime. In contrast, the Komodo dragon of Indonesia is a lizard

(b) Tuatara (*Sphenodon punctatus*)





(d) Wagler's pit viper (*Tropidolaemus wagleri*)



(c) Australian thorny devil lizard (*Moloch horridus*)

(e) American alligator (*Alligator mississippiensis*)



that can reach a length of 3 m. It hunts deer and other large prey, delivering venom with its bite.

Snakes descended from lizards with legs (see Figure 26.1); thus they are classified as legless lizards. Today, some species of snakes retain vestigial pelvic and limb bones, providing evidence of their ancestry. Despite their lack of legs, snakes are quite proficient at moving on land, most often by producing waves of lateral bending that pass from head to tail. Force exerted by the bends against solid objects pushes the snake forward. Snakes can also move by gripping the ground with their belly scales at several points along the body while the scales at intervening points are lifted slightly off the ground and pulled forward.

Snakes are carnivorous, and a number of adaptations aid them in hunting and eating prey. They have acute chemical sensors, and though they lack eardrums, they are sensitive to ground vibrations, which helps them detect the movements of prey. Heat-detecting organs between the eyes and nostrils of pit vipers, including rattlesnakes, are sensitive to minute temperature changes, enabling these night hunters to locate warm animals. Venomous snakes inject their toxin through a pair of sharp teeth that may be hollow or grooved. The flicking tongue is not venomous but helps fan odors toward olfactory (smell) organs on the roof of the mouth. Loosely articulated jawbones and elastic skin enable most snakes to swallow prey larger than the diameter of the snake's head (see Figure 23.14).

Next, we'll turn to the third (and final) clade of reptiles with living members, the archosaurs. There are two extant groups of archosaurs: the crocodilians and the birds.

Crocodilians

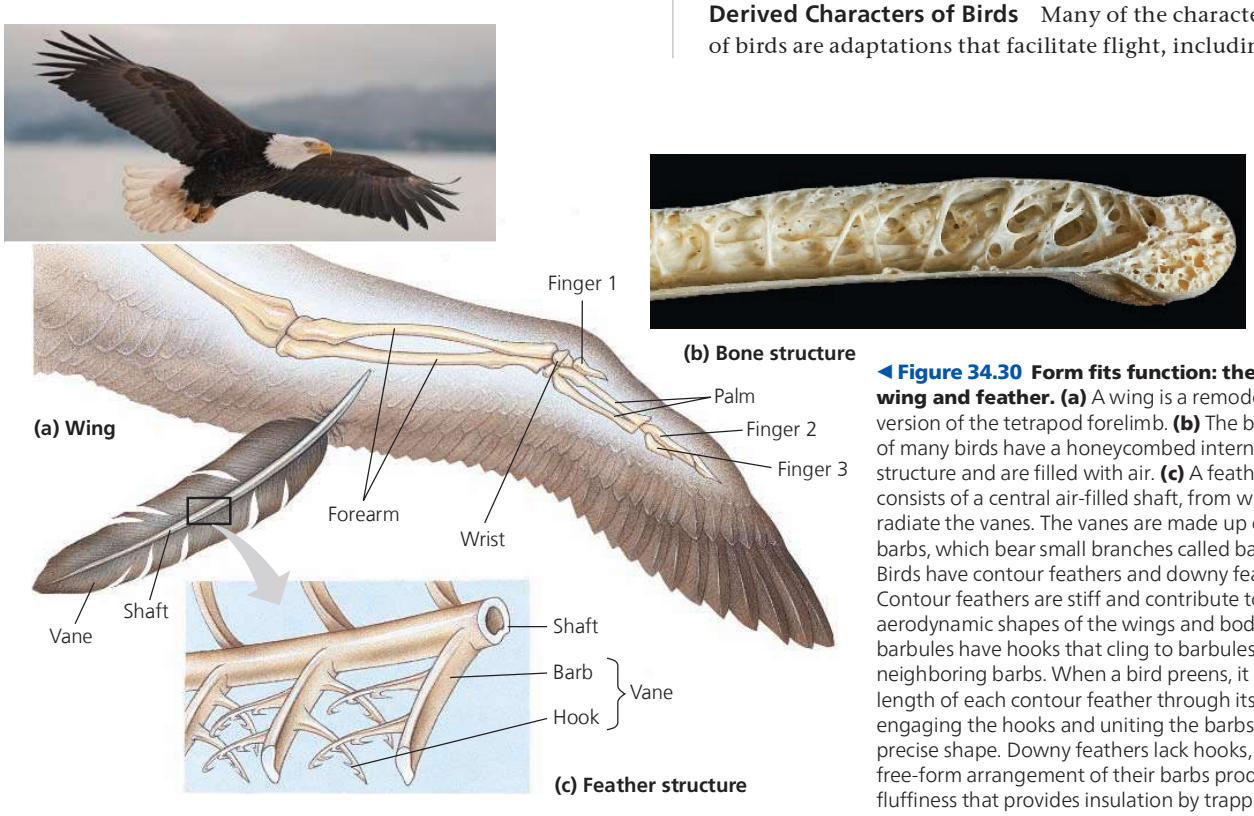
Alligators and crocodiles (collectively called crocodilians) belong to a lineage that reaches back to the late Triassic. The earliest members of this lineage were small terrestrial quadrupeds with long, slender legs. Later species became larger and adapted to aquatic habitats, breathing air through their upturned nostrils. Some Mesozoic crocodilians grew as long as 12 m and may have attacked dinosaurs and other prey at the water's edge.

The 24 known species of living crocodilians are confined to warm regions of the globe. In the southeastern United States, the American alligator **(Figure 34.29e)** has made a comeback after spending years on the endangered species list.

Birds

There are about 10,000 species of birds in the world. Like crocodilians, birds are archosaurs, but almost every feature of their anatomy has been modified in their adaptation to flight **(Figure 34.30)**.

Derived Characters of Birds Many of the characters of birds are adaptations that facilitate flight, including



◀ Figure 34.30 Form fits function: the avian wing and feather. (a) A wing is a remodeled version of the tetrapod forelimb. **(b)** The bones of many birds have a honeycombed internal structure and are filled with air. **(c)** A feather consists of a central air-filled shaft, from which radiate the vanes. The vanes are made up of barbs, which bear small branches called barbules. Birds have contour feathers and downy feathers. Contour feathers are stiff and contribute to the aerodynamic shapes of the wings and body. Their barbules have hooks that cling to barbules on neighboring barbs. When a bird preens, it runs the length of each contour feather through its beak, engaging the hooks and uniting the barbs into a precise shape. Downy feathers lack hooks, and the free-form arrangement of their barbs produces a fluffiness that provides insulation by trapping air.

Mastering Biology Video: Soaring Hawk

weight-saving modifications that make flying more efficient. For example, birds lack a urinary bladder, and the females of most species have only one ovary. The gonads of both females and males are usually small, except during the breeding season, when they increase in size. Living birds are also toothless, an adaptation that trims the weight of the head.

A bird's most obvious adaptations for flight are its wings and feathers (see Figure 34.30). Feathers are made of the protein β-keratin, which is also found in the scales of other reptiles. The shape and arrangement of the feathers form the wings into airfoils, and they illustrate some of the same principles of aerodynamics as the wings of an airplane. Power for flapping the wings comes from contractions of large pectoral (breast) muscles anchored to a keel on the sternum (breastbone). Some birds, such as eagles and hawks, have wings adapted for soaring on air currents and flap their wings only occasionally; other birds, including hummingbirds, must flap continuously to stay aloft (see Figure 34.34). Among the fastest birds are the appropriately named swifts, which can fly at speeds up to 170 km/hr.

Flight provides numerous benefits. It enhances scavenging and hunting, including enabling many birds to feed on flying insects, an abundant, nutritious food resource. Flight also provides ready escape from earthbound predators and enables some birds to migrate great distances to exploit different food resources and seasonal breeding areas.

Flying requires a great expenditure of energy from an active metabolism. Birds are endothermic; they use their own metabolic heat to maintain a high, constant body temperature. Feathers and in some species a layer of fat provide insulation that enables birds to retain body heat. The lungs have tiny tubes leading to and from elastic air sacs that improve airflow and oxygen uptake. This efficient respiratory system and a circulatory system with a four-chambered heart keep tissues well supplied with oxygen and nutrients, supporting a high rate of metabolism.

Flight also requires both acute vision and fine muscle control. Birds have color vision and excellent eyesight. The visual and motor areas of the brain are well developed, and the brain is proportionately larger than those of amphibians and nonbird reptiles.

Birds generally display very complex behaviors, particularly during breeding season, when they engage in elaborate courtship rituals. Because eggs have shells by the time they are laid, fertilization must be internal. Copulation usually involves contact between the openings to the birds' cloacas. After eggs are laid, the avian embryo must be kept warm through brooding by the mother, the father, or both, depending on the species.

The Origin of Birds Cladistic analyses of birds and reptilian fossils indicate that birds belong to the group of bipedal saurischian dinosaurs called theropods. Since the late 1990s, Chinese paleontologists have unearthed a spectacular trove of feathered theropod fossils that are shedding light on the origin of birds. Several species of dinosaurs closely related to birds had feathers with vanes, and a wider range of species had filamentous feathers. Such findings imply that feathers evolved long before powered flight. Among the possible functions of these early feathers were insulation, camouflage, and courtship display.

By about 160 million years ago, a lineage of feathered theropods had evolved into birds. Many researchers consider *Archaeopteryx*, which was discovered in a German limestone quarry in 1861, to be the earliest known bird **(Figure 34.31)**. It had feathered wings but retained ancestral characters such as teeth, clawed digits in its wings, and a long tail. *Archaeopteryx* flew well at high speeds, but unlike a present-day bird, it could not take off from a standing position. Fossils of later birds from the Cretaceous show a gradual loss of certain ancestral dinosaur features, such as teeth and clawed forelimbs, as well as the acquisition of innovations found in extant birds, including a short tail covered by a fan of feathers.

Living Birds Clear evidence of Neornithes, the clade that includes the 28 orders of living birds, can be found before the Cretaceous-Paleogene boundary 66 million years ago.

▼ Figure 34.31 Artist's reconstruction of the early bird *Archaeopteryx*. Fossil evidence indicates that *Archaeopteryx* was capable of powered flight but retained many characters of nonbird dinosaurs. Colors in this drawing were based on pigments extracted from fossilized *Archaeopteryx* feathers.



Mastering Biology HHMI Video: Great Transitions: The Origin of Birds

▼ Figure 34.32 An emu (*Dromaius novaehollandiae*), a flightless bird native to Australia.



Several groups of living and extinct birds include one or more flightless species. The **ratites**, an order of birds that includes the ostrich, rhea, kiwi, cassowary, and emu, are all flightless **(Figure 34.32)**. In ratites, the sternal keel is absent, and the pectoral muscles are small relative to those of birds that can fly.

Penguins make up another flightless order of birds, but, like flying birds, they have powerful pectoral muscles. They use these muscles to "fly" in the water: As they swim, they flap their flipper-like wings in a manner that resembles the flight stroke of a more typical bird **(Figure 34.33)**. Certain species of rails, ducks, and pigeons are also flightless.

Although the demands of flight have rendered the general body forms of many flying birds similar to one another, experienced bird-watchers can distinguish species by their profile, colors, flying style, behavior, and beak shape. The skeleton of a hummingbird's wing is

▼ Figure 34.33 A king penguin (*Aptenodytes patagonicus*) "flying" underwater. With their streamlined shape and powerful pectoral muscles, penguins are fast and agile swimmers.



▼ Figure 34.34 Hummingbird feeding while hovering. A hummingbird can rotate its wings in all directions, enabling it to hover and fly backward.



▼ Figure 34.35 A specialized beak. This American flamingo (*Phoenicopterus ruber*) dips its beak into the water and strains out the food.



unique, making it the only bird that can hover and fly backward **(Figure 34.34)**. Adult birds lack teeth, but during the course of avian evolution their beaks have taken on a variety of shapes suited to different diets. Some birds, such as parrots, have crushing beaks with which they can crack open hard nuts and seeds. Other birds, such as flamingoes, are filter feeders. Their beaks have "strainers" that enable them to capture food particles from the water **(Figure 34.35)**. Foot structure, too, shows considerable variation. Various birds use their feet for perching on branches **(Figure 34.36)**, grasping food, defense, swimming or walking, and even courtship (see Figure 24.3e).

▼ Figure 34.36 Feet adapted to perching. This great tit (*Parus major*) is a member of the Passeriformes, the perching birds. The toes of these birds can lock around a branch or wire, enabling the bird to rest for long periods.



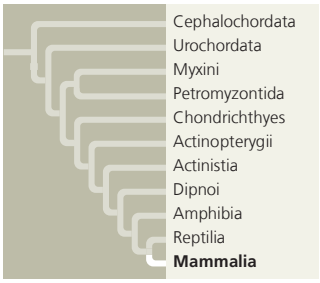
CONCEPT CHECK 34.5

1. Describe three key amniote adaptations for life on land.
2. Are snakes tetrapods? Explain.
3. Identify four avian adaptations for flight.
4. **VISUAL SKILLS** Based on the phylogeny shown in Figure 34.25, identify the sister group for (a) reptiles, (b) squamates, and (c) the clade that includes crocodilians and birds.

For suggested answers, see Appendix A.

CONCEPT 34.6

Mammals are amniotes that have hair and produce milk



The reptiles we have been discussing represent one of the two living lineages of amniotes. The other amniote lineage is our own, the **mammals**. Today, there are about 6,400 known species of mammals on Earth.

Derived Characters of Mammals

Mammals are named for their distinctive mammary glands, which produce milk for offspring. All mammalian mothers nourish their young with milk, a balanced diet rich in fats, sugars, proteins, minerals, and vitamins. Hair, another mammalian character, and a fat layer under the skin provide insulation that can conserve water and protect the body against extremes of heat or cold. Another mammalian adaptation for life on land is the kidney (see Figure 44.13), which is efficient at conserving water when removing wastes from the body. Some mammals, such as kangaroo rats, are so adept at conserving water that they can survive in arid environments while drinking little or no water at all **(Figure 34.37)**.

▼ Figure 34.37 Adaptations of the kangaroo rat to its extremely dry habitat.



MAKE CONNECTIONS *Explain how the catabolic pathways mentioned in 4 could provide a kangaroo rat with water. (See Concept 9.1.)*

Like birds, mammals are endothermic, and most have a high metabolic rate. Efficient respiratory and circulatory systems (including a four-chambered heart) support a mammal's metabolism. Also as in birds, mammals generally have a larger brain than other vertebrates of equivalent size, and many species are capable learners. The relatively long duration of parental care extends the time for offspring to learn important survival skills by observing their parents. In addition, whereas the teeth of reptiles are generally uniform in size and shape, the jaws of mammals typically bear a variety of teeth with sizes and shapes adapted for chewing many kinds of foods. Humans, like most mammals, have teeth modified for shearing (incisors and canine teeth) and for crushing and grinding (premolars and molars).

Early Evolution of Mammals

Mammals belong to a group of amniotes known as **synapsids**. Early nonmammalian synapsids lacked hair, had a sprawling gait, and laid eggs. A distinctive characteristic of synapsids is the single temporal fenestra, a hole behind the eye socket on each side of the skull. Humans retain this feature; your jaw muscles pass through the temporal fenestra and anchor on your temple. Fossil evidence shows that the

jaw was remodeled as mammalian features arose gradually in successive lineages of earlier synapsids (see Figure 25.7); in all, these changes took more than 100 million years. In addition, two of the bones that formerly made up the jaw joint (the quadrate and the articular) were incorporated into the mammalian middle ear **(Figure 34.38)**. This evolutionary change is reflected in changes that occur during development. For example, as a mammalian embryo grows, the posterior region of its jaw—which in a reptile forms the articular bone—can be observed to detach from the jaw and migrate to the ear, where it forms the malleus.

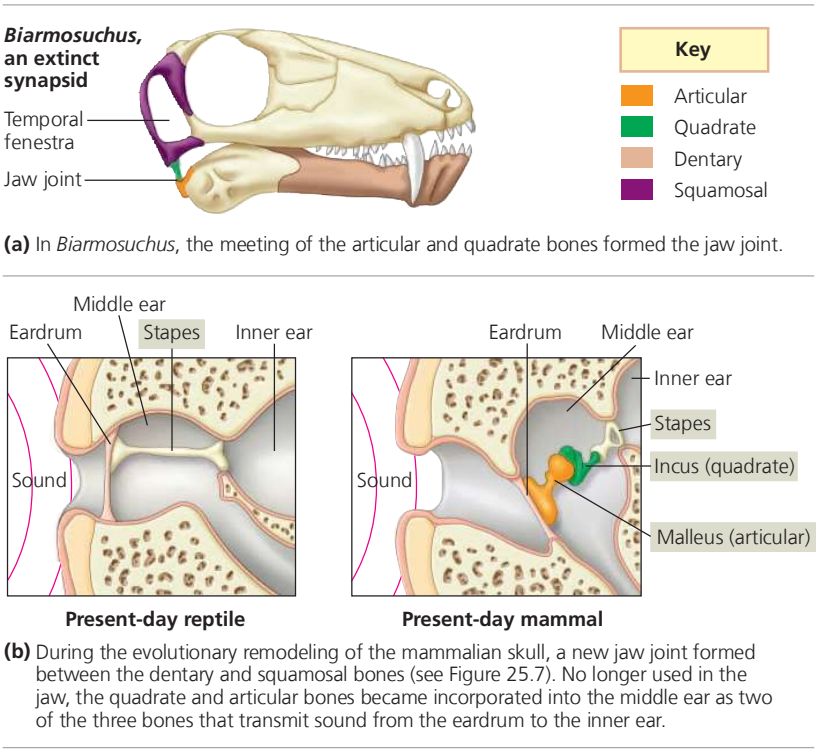
Synapsids evolved into large herbivores and carnivores during the Permian period (299–252 million years ago), and for a time they were the dominant tetrapods. However, the Permian-Triassic extinctions took a heavy toll on them, and their diversity fell during the Triassic (252–201 million years ago). Increasingly mammal-like synapsids emerged by the end of the Triassic. While not true mammals, these synapsids had acquired a number of the derived characters that distinguish mammals from other amniotes. They were small and probably hairy, and they likely fed on insects at night. Their bones show that they grew faster than other synapsids, suggesting that they probably had a relatively high metabolic rate; however, they still laid eggs.

During the Jurassic (201–145 million years ago), the first true mammals arose and diversified into many short-lived lineages. A diverse set of mammal species coexisted with dinosaurs in the Jurassic and Cretaceous periods, but most of these species were small, measuring less than 1 m in length. One factor that may have contributed to their small size is that dinosaurs already occupied many ecological niches of large-bodied animals.

Fossil and molecular evidence indicate that by 160 million years ago, the three major lineages of mammals had emerged: those leading to monotremes (egg-laying mammals), marsupials (mammals with a pouch), and eutherians (placental mammals). After the extinction of large dinosaurs, pterosaurs, and marine reptiles during the late Cretaceous period, mammals underwent an adaptive radiation, giving rise to large predators and herbivores as well as flying and aquatic species.

Monotremes

Monotremes are found only in Australia and New Guinea and are represented by one species of platypus and four species of echidnas (spiny anteaters; **Figure 34.39**). Monotremes lay eggs, a character that is ancestral for amniotes and retained in most reptiles. Like all mammals, monotremes have hair and produce milk, but they lack nipples. Milk is secreted by glands on the belly of the mother. After hatching, the baby sucks the milk from the mother's fur.



(a) In *Biarmosuchus*, the meeting of the articular and quadrate bones formed the jaw joint.

(b) During the evolutionary remodeling of the mammalian skull, a new jaw joint formed between the dentary and squamosal bones (see Figure 25.7). No longer used in the jaw, the quadrate and articular bones became incorporated into the middle ear as two of the three bones that transmit sound from the eardrum to the inner ear.

▶ Figure 34.38 The evolution of the mammalian ear bones. *Biarmosuchus* was a synapsid, a lineage that eventually gave rise to the mammals. Bones that transmit sound in the ear of mammals arose from the modification of bones in the jaw of nonmammalian synapsids.

MAKE CONNECTIONS *Review the definition of exaptation in Concept 25.6. Summarize the process by which exaptation occurs and explain how the incorporation of the articular and quadrate bones into the mammalian inner ear is an example.*

▼ Figure 34.39 Short-beaked echidna (*Tachyglossus aculeatus*), an Australian monotreme. Monotremes have hair and produce milk, but they lack nipples. Monotremes are the only mammals that lay eggs (inset).



Marsupials

Opossums, kangaroos, and koalas are examples of the group called **marsupials**. Both marsupials and eutherians share derived characters not found among monotremes. They have higher metabolic rates and nipples that provide milk, and they give birth to live young. The embryo begins development inside the uterus of the female's reproductive tract. The lining of the uterus and the extraembryonic membranes that arise from the embryo form a **placenta**, a structure in which nutrients diffuse into the embryo from the mother's blood.

A marsupial is born very early in its development and completes its embryonic development while nursing **(Figure 34.40a)**. In most species, the nursing young are held within a maternal pouch called a *marsupium*. A red kangaroo, for instance, is about the size of a honeybee at its birth, just 33 days after fertilization. Its back legs are merely buds, but its front legs are strong enough for it to crawl from the exit of its mother's reproductive tract to a pouch that opens to the front of her body, a journey that lasts a few minutes. In other species, the marsupium opens to the rear of the mother's body; in greater bilbies, this protects the young as their mother burrows in the dirt **(Figure 34.40b)**.

Marsupials existed worldwide during the Mesozoic era, but today they are found only in the Australian region and in the Americas **(Figure 34.40c)**. The biogeography of marsupials illustrates the interplay between biological and geologic evolution (see Concept 25.4). After the breakup of the supercontinent Pangaea, South America and Australia became island continents, and their marsupials diversified in isolation from the eutherians that began an adaptive radiation on the northern continents. Australia has not been in contact with another continent since early in the Cenozoic era, 66 million years ago. In Australia, convergent evolution has resulted in a diversity of marsupials that resemble eutherians in similar ecological roles in other

▼ Figure 34.40 Marsupials in Australia and North America.



(a) A young brushtail possum (Australia). The offspring of marsupials are born very early in their development. They finish their growth while nursing from a nipple (in their mother's pouch in most species).

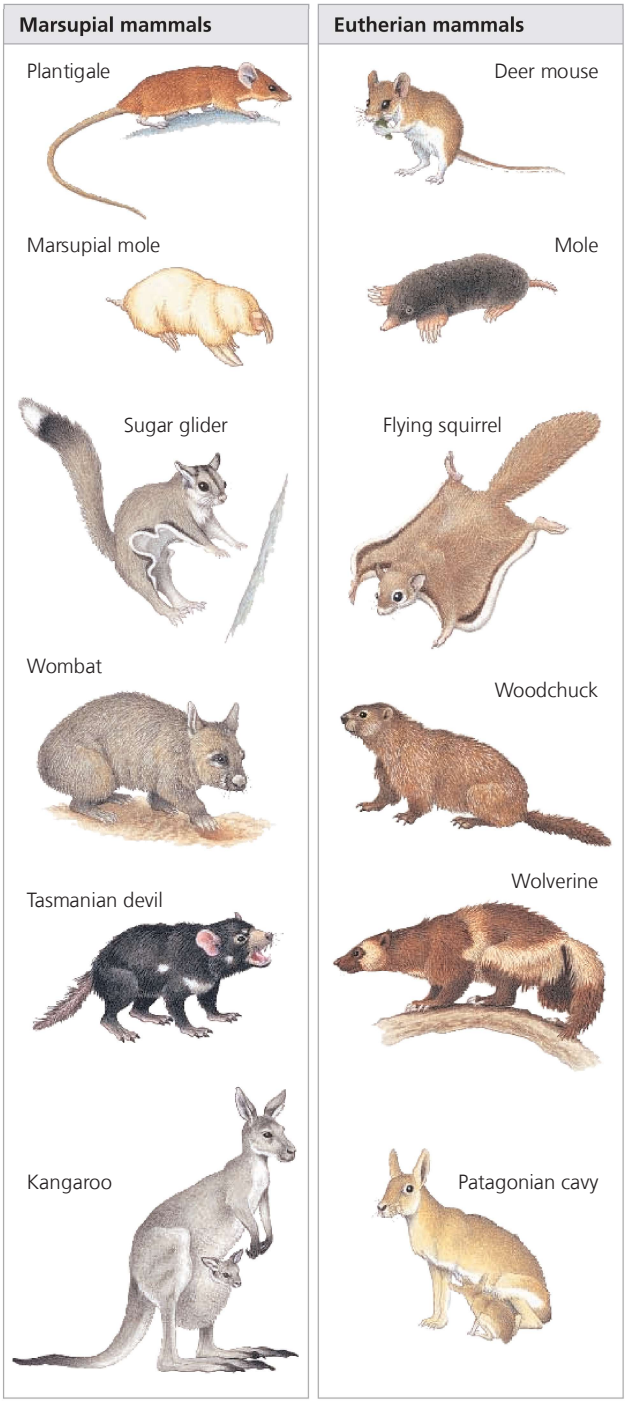


(b) A greater bilby (Australia). The greater bilby is a digger and burrower that eats termites and other insects, along with the seeds, roots, and bulbs of various plants. The female's rear-opening pouch helps protect the young from dirt as the mother digs. Other marsupials, such as kangaroos, have a pouch that opens to the front.



(c) Virginia opossum (Central and North America). This species is the only marsupial found north of Mexico. After the young complete development in the mother's pouch, they spend another four to five months riding on her back before living independently.

▼ Figure 34.41 Convergent evolution of marsupials and eutherians (placental mammals). (Drawings not to scale.)



parts of the world **(Figure 34.41)**. In contrast, although South America had a diverse marsupial fauna throughout the Paleogene, it has experienced several immigrations of eutherians. One of the most important occurred about 3 million years ago, when North and South America joined at the Panamanian isthmus and extensive two-way traffic of animals took place over the land bridge. Today, only three families of marsupials live outside the Australian region, and the only marsupials found in the wild in North America are a few species of opossum.

Eutherians (Placental Mammals)

Eutherians are commonly called placental mammals because their placentas are more complex than those of marsupials. Eutherians have a longer pregnancy than marsupials. Young eutherians complete their embryonic development within the uterus, joined to their mother by the placenta. The eutherian placenta provides an intimate and long-lasting association between the mother and her developing young.

The major groups of living eutherians are thought to have diverged from one another in a burst of evolutionary change. The timing of this burst is uncertain: Molecular data suggest it occurred about 100 million years ago, while morphological data suggest it was about 60 million years ago. **Figure 34.42** explores several major eutherian orders and their phylogenetic relationships with each other as well as with the monotremes and marsupials.

Primates

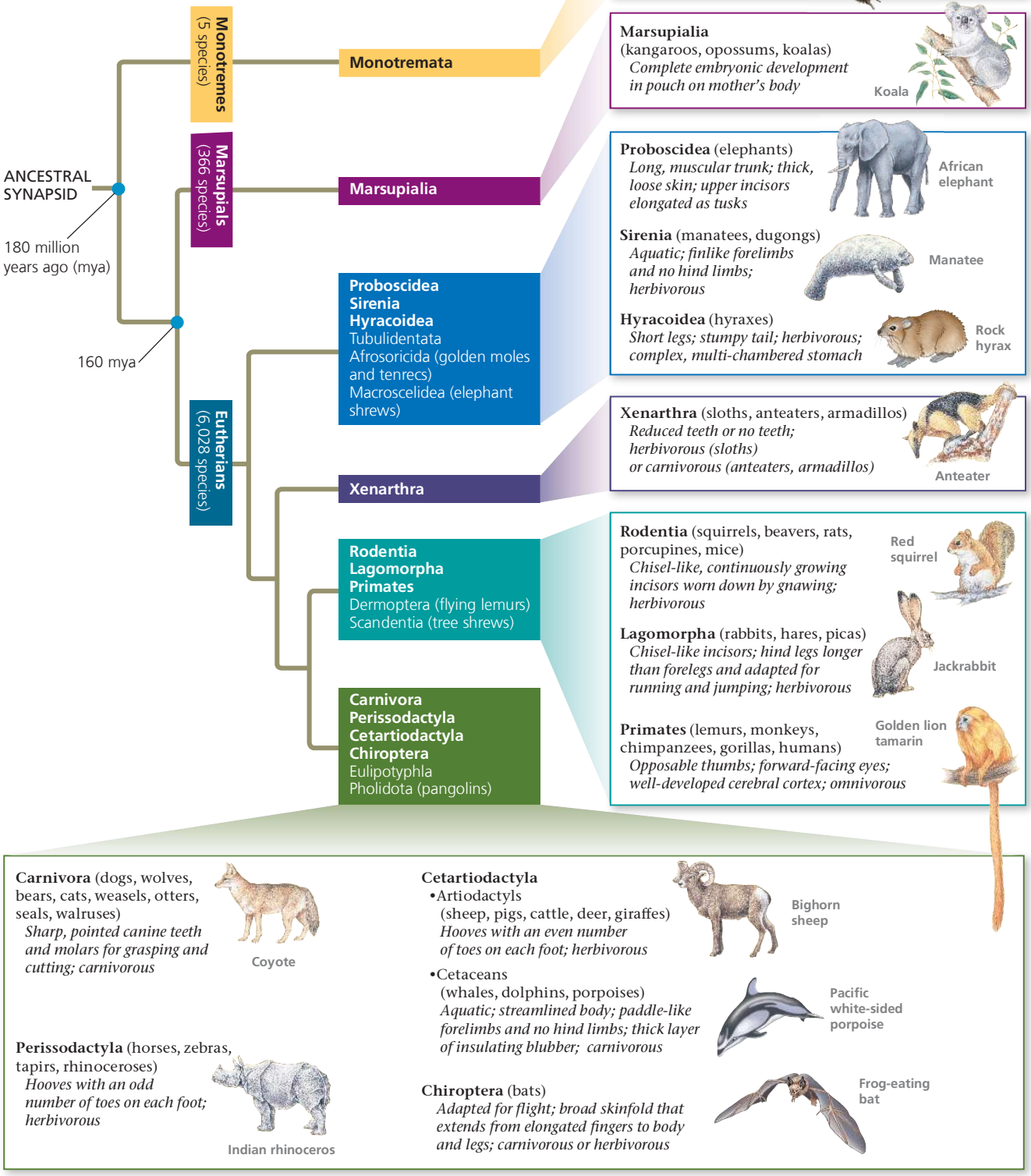
The mammalian order Primates includes the lemurs, tarsiers, monkeys, and apes. Humans are members of the ape group.

Derived Characters of Primates Most primates have hands and feet adapted for grasping, and their digits have flat nails instead of the narrow claws of other mammals. There are other characteristic features of the hands and feet, too, such as skin ridges on the fingers (which account for human fingerprints). Relative to other mammals, primates have a large brain and short jaws, giving them a flat face. Their forward-looking eyes are close together on the front of the face. Primates also exhibit relatively well-developed parental care and complex social behavior.

The earliest known primates were tree-dwellers, and many of the characteristics of primates are adaptations to the demands of living in the trees. Grasping hands and feet allow primates to hang onto tree branches. All living primates except humans have a big toe that is widely separated from the other toes, enabling them to grasp branches with their feet. All primates also have a thumb that is relatively movable and separate from the fingers, but monkeys and apes have a fully **opposable thumb**; that is, they can touch the ventral surface (fingerprint side) of the tip of all four fingers with the ventral surface of the thumb of the same hand. In monkeys and apes other than humans, the opposable thumb functions in a grasping "power grip." In humans, a distinctive bone structure at the base of the thumb allows it to be used for more precise manipulation. The unique dexterity of humans represents descent with modification from our tree-dwelling

▼ Figure 34.42 Exploring Mammalian Diversity

One hypothesis for the evolutionary relationships of mammals, represented by the tree shown here, clusters the eutherian orders into four main clades. All 20 extant orders of mammals are listed; the orders in bold type are surveyed in more detail around the tree.





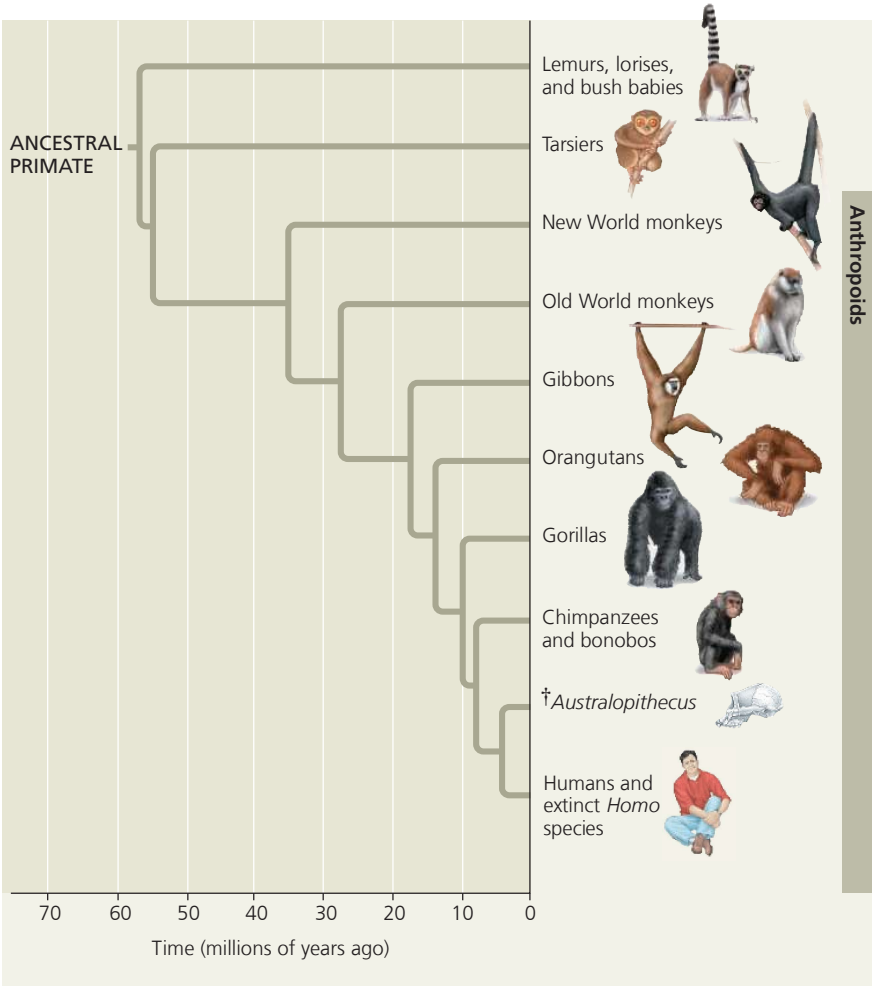
◀ Figure 34.43 Verreaux's sifakas (*Propithecus verreauxi*), a type of lemur.

ancestors. Arboreal maneuvering also requires excellent eye-hand coordination. The overlapping visual fields of the two forward-facing eyes enhance depth perception, an obvious advantage when brachiating (traveling by swinging from branch to branch in trees).

Living Primates There are three main groups of living primates: (1) the lemurs of Madagascar **(Figure 34.43)** and the lorises and bush babies of tropical Africa and southern Asia; (2) the tarsiers, which live in southeastern Asia; and (3) the **anthropoids**, which include monkeys and apes and are found worldwide. The first group—lemurs, lorises, and bush babies—probably resemble early arboreal primates. The oldest known tarsier fossils date to 55 million years ago; along with DNA evidence, these fossils indicate that tarsiers are more closely related to anthropoids than to the lemur group **(Figure 34.44)**.

You can see in Figure 34.44 that monkeys do not form a clade but rather consist of two groups, the New and Old World monkeys. Both of these groups are thought to have originated in Africa or Asia. The fossil record indicates that New World monkeys first colonized South America roughly 25 million years ago. By that time, South America and Africa had drifted apart, and monkeys may have reached South America from Africa by rafting on logs or other debris. What is certain is that New World monkeys and Old World monkeys underwent separate adaptive radiations during their many millions of years of separation **(Figure 34.45)**. All species of New World monkeys are arboreal, whereas Old World monkeys include ground-dwelling as well as arboreal species. Most monkeys in both groups are diurnal (active during the day) and usually live in bands held together by social behavior.

The other group of anthropoids consists of primates informally called apes **(Figure 34.46)**. The ape group includes four genera of gibbons, along with the so-called "great apes," the genera *Pongo* (orangutans), *Gorilla* (gorillas), *Pan* (chimpanzees and bonobos), and *Homo* (humans). The apes diverged from Old World monkeys

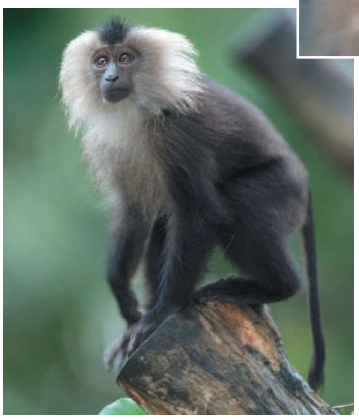


▲ Figure 34.44 A phylogenetic tree of primates. The fossil record indicates that the lineage leading to monkeys and apes diverged from other primates 55 million years ago. The lineage leading to humans and *Australopithecus* branched off from other apes about 8 million years ago; the dagger symbol (†) denotes an extinct group.

VISUAL SKILLS *Is the phylogeny shown here consistent with the idea that humans evolved from chimpanzees? Explain.*



(a) New World monkeys, such as spider monkeys (shown here), squirrel monkeys, and capuchins, have a prehensile tail (one adapted for grasping) and nostrils that open to the sides.



(b) Old World monkeys lack a prehensile tail, and their nostrils open downward. This group includes macaques (shown here), mandrils, baboons, and rhesus monkeys.

▲ Figure 34.45 New World monkeys and Old World monkeys.

about 25–30 million years ago. Today, nonhuman apes are found exclusively in tropical regions of the Old World. With the exception of gibbons, living apes are larger than either New or Old World monkeys. All living apes have relatively long arms, short legs, and no tail. Although all nonhuman apes spend time in trees, only gibbons and orangutans are primarily arboreal. Social organization varies among the apes; gorillas and chimpanzees are highly social. Finally, compared to other primates, apes have a larger brain in proportion to their body size, and their behavior is more flexible. These two characteristics are especially prominent in our next group, the hominins.

CONCEPT CHECK 34.6

1. Contrast monotremes, marsupials, and eutherians in terms of how they bear young.
2. Identify at least five derived traits of primates.
3. **MAKE CONNECTIONS** Develop a hypothesis to explain why the diversity of mammals increased in the Cenozoic. Your explanation should consider mammalian adaptations as well as factors such as mass extinctions and continental drift (review Concept 25.4).

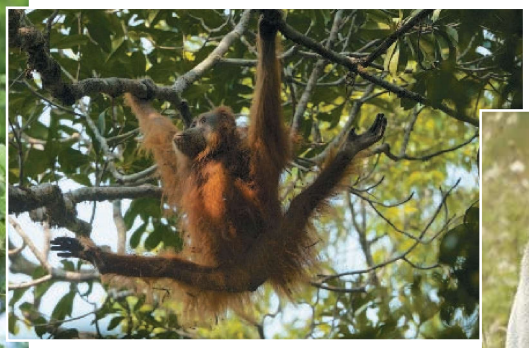
For suggested answers, see Appendix A.

▼ Figure 34.46 Nonhuman apes.

(a) Gibbons (18 species), such as this Muller's gibbon, are found only in south-eastern Asia. Their very long arms and fingers are adaptations for brachiating (swinging by the arms from branch to branch).



(b) Orangutans (3 species) are shy apes that live in the rain forests of Sumatra and Borneo. Named in 2017, this species (*Pongo tapanuliensis*) is the first great ape discovered in nearly 100 years.

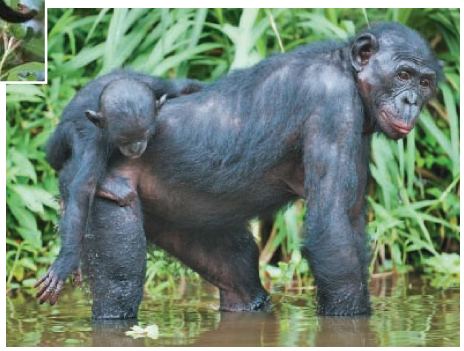


(c) Gorillas (2 species) are the largest apes; some males are almost 2 m tall and weigh about 200 kg. Found only in Africa, these herbivores usually live in groups of up to about 20 individuals.





(d) Chimpanzees live in tropical Africa. They feed and sleep in trees but also spend a great deal of time on the ground. Chimpanzees are intelligent, communicative, and social.



(e) Bonobos are in the same genus (*Pan*) as chimpanzees but are smaller. They survive today only in the African nation of Congo.

Mastering Biology **Videos: Chimp Cracking Nut • Gibbons Brachiating**

CONCEPT 34.7

Humans are mammals that have a large brain and bipedal locomotion

In our tour of Earth's biodiversity, we turn now to our own species, *Homo sapiens*, which is about 200,000 years old. When you consider that life has existed on Earth for at least 3.5 billion years, we are clearly evolutionary newcomers.

Derived Characters of Humans

Many characters distinguish humans from other apes. Most obviously, humans stand upright and are bipedal (walk on two legs). Humans have a much larger brain and are capable of language, symbolic thought, artistic expression, and the manufacture and use of complex tools. Humans also have reduced jawbones and jaw muscles, along with a shorter digestive tract.

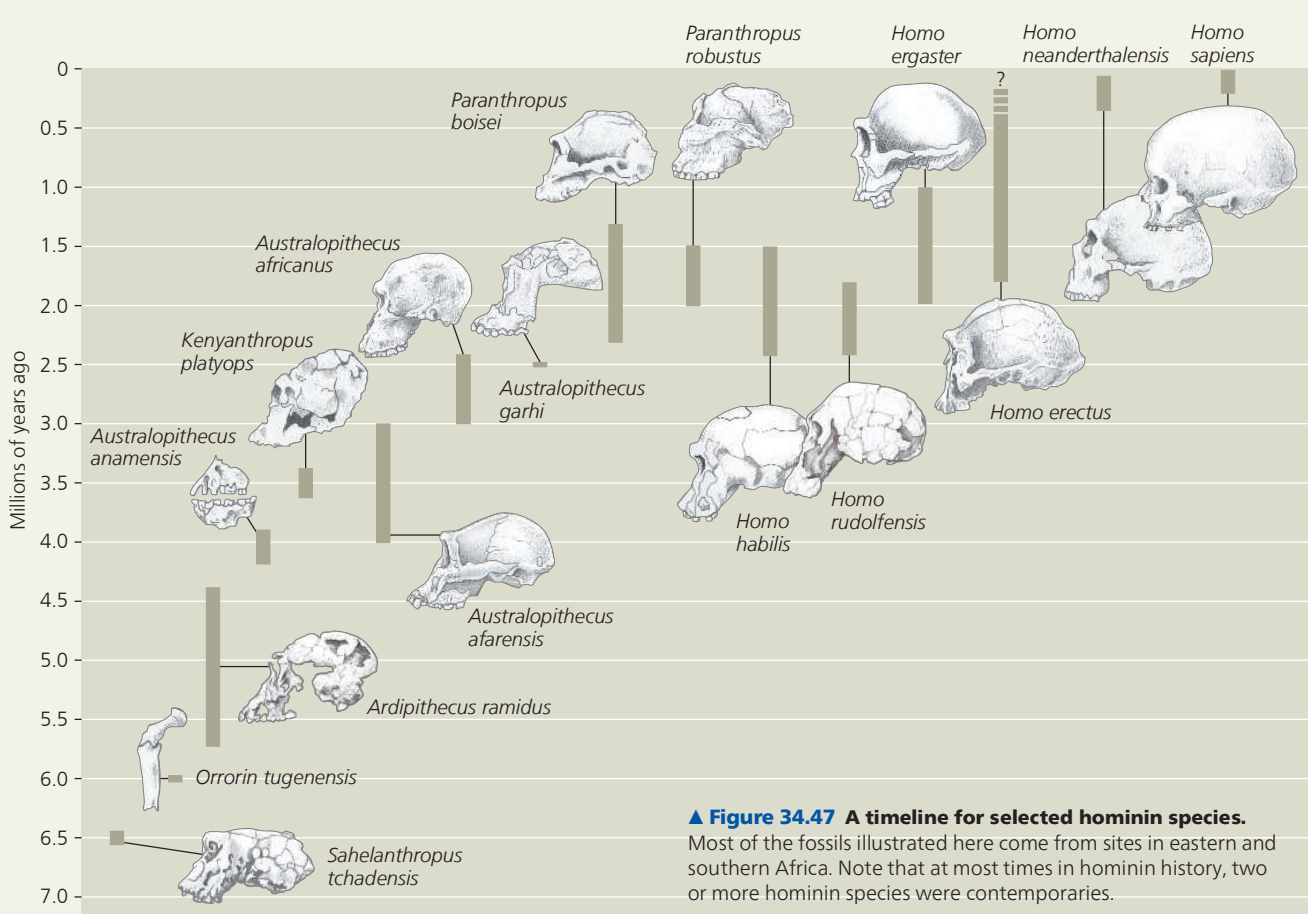
At the molecular level, the list of derived characters of humans is growing as scientists compare the human and chimpanzee genomes. Although the two genomes are 99% identical, a difference of 1% can represent many changes in a genome with 3 billion base pairs. Furthermore, changes in a small number of genes can have large effects. This point was highlighted by recent results showing that humans and chimpanzees differ in the expression of 19 regulatory genes. These genes turn other genes on and off and hence may account for many differences between humans and chimpanzees.

Bear in mind that such genomic differences—and whatever derived phenotypic traits they encode—separate humans from other *living* apes. But many of these new characters first emerged in our ancestors, long before our own species appeared. We will consider some of these ancestors to see how these characters originated.

Mastering Biology **HHMI Video: Great Transitions: The Origin of Humans**

The Earliest Hominins

The study of human origins is known as **paleoanthropology**. Paleoanthropologists have unearthed fossils of approximately 25 extinct species that are more closely related to humans than to chimpanzees. These species are known as **hominins** **(Figure 34.47)**. Since 1994, fossils of four hominin species



▲ Figure 34.47 A timeline for selected hominin species. Most of the fossils illustrated here come from sites in eastern and southern Africa. Note that at most times in hominin history, two or more hominin species were contemporaries.

dating to more than 4 million years ago have been discovered. The oldest of these hominins, *Sahelanthropus tchadensis*, lived about 6.5 million years ago.

Sahelanthropus and other early hominins shared some of the derived characters of humans. For example, they had reduced canine teeth, and some fossils suggest that they had relatively flat faces. They also show signs of having been more upright and bipedal than other apes. One clue to their upright stance can be found in the foramen magnum, the hole at the base of the skull through which the spinal cord passes. In chimpanzees, the foramen magnum is relatively far back on the skull, while in early hominins (and in humans), it is located underneath the skull. This position allows us to hold our head directly over our body, as early hominins apparently did as well. The pelvis, leg bones, and feet of the 4.4-million-year-old *Ardipithecus ramidus* also suggest that early hominins were increasingly bipedal **(Figure 34.48)**. (We will return to the subject of bipedalism later in the chapter.)

Note that the characters that distinguish humans from other living apes did not all evolve in tight unison. While early hominins were showing signs of bipedalism, their brains remained small—about 300–450 cm^3 in volume, compared with an average of 1,300 cm^3 for *Homo sapiens*. The earliest hominins were also small overall. *A. ramidus*, for example, is estimated to have been about 1.2 m tall, with relatively large teeth and a jaw that projected beyond the upper part of the face. Humans, in contrast, average about 1.7 m in height and have a relatively flat face; compare your own face with that of the chimpanzees in Figure 34.46d.

▼ Figure 34.48 "Ardi," a 4.4-million-year-old fossil of *Ardipithecus ramidus*.



It's important to avoid two common misconceptions about early hominins. One is to think of them either as chimpanzees or as having evolved from chimpanzees. Chimpanzees represent the tip of a separate branch of evolution, and they acquired derived characters of their own after they diverged from their common ancestor with humans.

Another misconception is to think of human evolution as a ladder leading directly from an ancestral ape to *Homo sapiens*. This error is often illustrated as a parade of fossil species that become progressively more like ourselves as they march across the page. If human evolution is a parade, it is a very disorderly one, with many groups breaking away to wander other evolutionary paths. At times, several hominin species coexisted. These species often differed in skull shape, body size, and diet (as inferred from their teeth). Ultimately, all but one lineage—the one that gave rise to *Homo sapiens*—ended in extinction. Overall, considering the characteristics of all hominins that lived over the past 6.5 million years, *H. sapiens* appears not as the end result of a straight evolutionary path, but rather as the only surviving member of a highly branched evolutionary tree.

Australopiths

The fossil record indicates that hominin diversity increased dramatically between 4 and 2 million years ago. Many of the hominins from this period are collectively called australopiths. Their phylogeny remains unresolved on many points, but as a group, they are almost certainly paraphyletic. The earliest member of the group, *Australopithecus anamensis*, lived 4.2–3.9 million years ago, close in time to older hominins such as *Ardipithecus ramidus*.

Australopiths got their name from the 1924 discovery in South Africa of *Australopithecus africanus* ("southern ape of Africa"), which lived between 3 and 2.4 million years ago. With the discovery of more fossils, it became clear that *A. africanus* walked fully erect (was bipedal) and had human-like hands and teeth. However, its brain was only about one-third the size of the brain of a present-day human.

In 1974, in the Afar region of Ethiopia, scientists discovered a 3.2-million-year-old *Australopithecus* skeleton that was 40% complete. "Lucy," as the fossil was named, was short—only about 1 m tall. Lucy and similar fossils have been given the species name *Australopithecus afarensis* (for the Afar region). Fossil evidence shows that *A. afarensis* existed as a species for at least 1 million years.

At the risk of oversimplifying, we could say that *A. afarensis* had fewer of the derived characters of humans above the neck than below. Lucy's brain was the size of a softball, a size similar to that expected for a chimpanzee of Lucy's body size. *A. afarensis* skulls also have a long lower jaw. Skeletons of *A. afarensis* suggest that these hominins were capable of arboreal locomotion, with arms that were relatively long in proportion to body size (compared to the proportions in humans). However, fragments of pelvic and skull bones indicate that *A. afarensis* walked on two legs. Fossilized footprints in Laetoli, Tanzania, corroborate the skeletal evidence that hominins living at the time of *A. afarensis* were bipedal **(Figure 34.49)**.

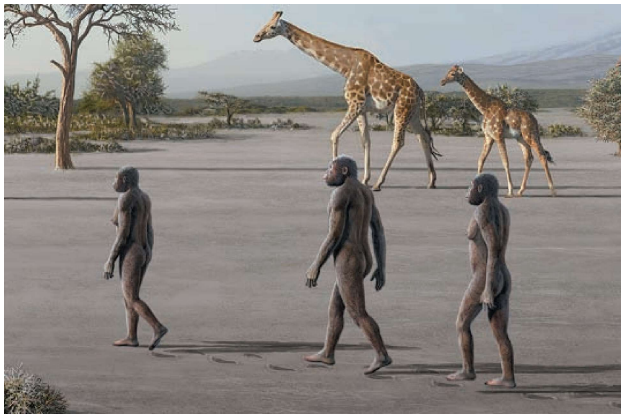
Another lineage of australopiths consisted of the "robust" australopiths. These hominins, which included species such as *Paranthropus boisei*, had sturdy skulls with powerful jaws



▶ Figure 34.49 Evidence that hominins walked upright 3.5 million years ago.

(a) The Laetoli footprints, more than 3.5 million years old, confirm that upright posture evolved quite early in hominin history.

(b) An artist's reconstruction of *A. afarensis*, a hominin alive at the time of the Laetoli footprints.



and large teeth, adapted for grinding and chewing hard, tough foods. They contrast with the "gracile" (slender) australopiths, including *A. afarensis* and *A. africanus*, which had lighter feeding equipment adapted for softer foods.

Combining evidence from the earliest hominins with the much richer fossil record of later australopiths makes it possible to formulate hypotheses about significant trends in hominin evolution. In the **Scientific Skills Exercise**, you'll examine one such trend: how hominin brain volume has changed over time. Here we'll consider two other trends: the emergence of bipedalism and tool use.

Bipedalism

Our anthropoid ancestors of 30–35 million years ago were still tree-dwellers. By about 10 million years ago, the Himalayan mountain range had formed, thrust up in the aftermath of the Indian plate's collision with the Eurasian plate (see Figure 25.16). The climate became drier, and the forests of what are now Africa and Asia contracted. The result was an increased area of savanna (grassland) habitat, with fewer trees. Researchers have hypothesized that as the habitat changed, natural selection may have favored adaptations that made moving over open ground more efficient. Underlying this idea is the fact that while nonhuman apes are superbly adapted for climbing trees, they are less well suited for ground travel. For example, as a chimpanzee walks, it uses four times the amount of energy used by a human.

Although elements of this hypothesis survive, the picture now appears more complex. Even though all fossils of early hominins show indications of bipedalism, none of these hominins lived in savannas. Instead, they lived in mixed habitats ranging from forests to open woodlands. Furthermore, whatever the selective pressure that led to bipedalism, hominins did not become more bipedal in a simple, linear fashion. *Ardipithecus* had skeletal elements indicating that it could switch to upright walking but also was well suited for climbing trees. Australopiths seem to have had various locomotor styles, and some species spent more time on the ground than others. Only about 1.9 million years ago did hominins begin to walk long distances on two legs. These hominins lived in more arid environments, where bipedal walking requires less energy than walking on all fours.

Tool Use

As you read earlier, the manufacture and use of complex tools are derived behavioral characters of humans. Determining the origin of tool use in hominin evolution is very difficult. Other apes are capable of surprisingly sophisticated tool use. Orangutans, for example, can fashion sticks into probes for retrieving insects from their nests. Chimpanzees are even more adept, using rocks to smash open food and putting leaves on their feet to walk over thorns. It's likely that early hominins were capable of this sort of simple tool use, but finding fossils of modified sticks or leaves that were used as shoes is practically impossible.

The oldest generally accepted evidence of tool use by hominins is 2.5-million-year-old cut marks on animal bones found in Ethiopia. These marks suggest that hominins cut flesh from the bones of animals using stone tools. Interestingly, the hominins whose fossils were found near the site where the bones were discovered had a relatively small brain. If these hominins, which have been named *Australopithecus garhi*, were in fact the creators of the stone tools used on the bones, that would suggest that stone tool use originated before the evolution of large brains in hominins.

Mastering Biology **HHMI Video: The Tool-Making Animal**

Early *Homo*

The earliest fossils that paleoanthropologists place in our genus, *Homo*, include those of the species *Homo habilis*. These fossils, ranging in age from about 2.4 to 1.6 million years, show clear signs of certain derived hominin characters above

Scientific Skills Exercise

Determining the Equation of a Regression Line



How Has Brain Volume Changed Over Time in the Hominin Lineage? The hominin taxon includes *Homo sapiens* and about 20 extinct species that are thought to represent early relatives of humans. Researchers have found that the brain volume of the earliest hominins ranged between 300 and 450 cm^3, similar to the brain volume of chimpanzees. The brain volumes of modern humans range between 1,200 and 1,800 cm^3. In this exercise, you'll examine how mean brain volume changed over time and across various hominin species.

How the Study Was Done In this table, x_i is the mean age of each hominin species, and y_i is the mean brain volume (cm^3). Ages with negative values represent millions of years before the present (which has an age of 0.0).

Hominin Species	Mean age (millions of years; x_i)	$x_i - \bar{x}$	Mean Brain Volume (cm^3; y_i)	$y_i - \bar{y}$	$(x_i - \bar{x}) \times (y_i - \bar{y})$
Ardipithecus ramidus	−4.4		325		
Australopithecus afarensis	−3.4		375		
Homo habilis	−1.9		550		
Homo ergaster	−1.6		850		
Homo erectus	−1.2		1,000		
Homo heidelbergensis	−0.5		1,200		
Homo neanderthalensis	−0.1		1,400		
Homo sapiens	0.0		1,350		

Data from Dean Falk, Florida State University, 2013.

INTERPRET THE DATA

How did the brain volume of hominin species change over time? In particular, is there a linear (straight-line) relationship between brain volume and time?

To find out, we'll perform a linear regression, a technique for determining the equation for the straight line that provides a "best fit" to a set of data. Recall that the equation for a straight line between two variables, x and y, is

$$y = mx + b$$

In this equation, m represents the slope of the line, while b represents the y-intercept (the point at which the straight line crosses the y-axis). When $m < 0$, the line has a negative slope, indicating that the values of y become *smaller* as values of x become *larger*. When $m > 0$, the line has a positive slope, meaning that the values of y become larger as values of x become larger. When $m = 0$, y has a constant value (b).

The correlation coefficient, r, can be used to calculate the values of m and b in a linear regression:

$$m = r\frac{s_y}{s_x} \quad \text{and} \quad b = \bar{y} - m\bar{x}.$$

In these equations, s_x and s_y are the standard deviations of variables x and y, respectively, while $\bar{x}$ and $\bar{y}$ are the means of those two variables. (See the Scientific Skills Exercise for Chapter 32 for more information about the correlation coefficient, mean, and standard deviation.)

1. Calculate the means ($\bar{x}$ and $\bar{y}$) from the $n = 8$ data points in the table. Next, fill in the $(x_i - \bar{x})$ and $(y_i - \bar{y})$ columns in the data table, and use those results to calculate the standard deviations s_x and s_y.
2. As described in the Scientific Skills Exercise for Chapter 32, the formula for a correlation coefficient is
$$r = \frac{\sum(x_i - \bar{x})(y_i - \bar{y})}{(n - 1)(s_x s_y)}$$
Fill in the column in the data table for the product $(x_i - \bar{x}) \times (y_i - \bar{y})$. Use these values and the standard deviations calculated in question 1 to calculate the correlation coefficient r between the brain volume of hominin species (y) and the ages of those species (x).
3. Based on the value of r that you calculated in question 2, describe in words the correlation between mean brain volume of hominin species and the mean age of the species.
4. **(a)** Use your calculated value of r to calculate the slope (m) and the y-intercept (b) of a regression line for this data set. **(b)** Graph the regression line for the mean brain volume of hominin species versus the mean age of the species. Be careful to select and label your axes correctly. **(c)** Plot the data from the table on the same graph that shows the regression line. Does the regression line appear to provide a reasonable fit to the data?
5. The equation for a regression line can be used to calculate the value of y expected for any particular value of x. For example, suppose that a linear regression indicated that $m = 2$ and $b = 4$. In this case, when $x = 5$, we expect that $y = 2x + 4 = (2 \times 5) + 4 = 14$. Based on the values of m and b that you determined in question 4, use this approach to determine the expected mean brain volume for a hominin that lived 4 million years ago (that is, $x = -4$).
6. The slope of a line can be defined as $m = \frac{y_2 - y_1}{x_2 - x_1}$, where (x_1, y_1) and (x_2, y_2) are the coordinates of two points on the line. As such, the slope represents the ratio of the rise of a line (how much the line rises vertically) to the run of the line (how much the line changes horizontally). Use the definition of the slope to estimate how long it took for mean brain volume to increase by 100 cm^3 over the course of hominin evolution.

Instructors: A version of this Scientific Skills Exercise can be assigned in **Mastering Biology.**

the neck. Compared to the australopiths, *H. habilis* had a shorter jaw and a larger brain volume, about 550–750 cm^3. Sharp stone tools have also been found with some fossils of *H. habilis* (the name means "handy man").

Fossils from 1.9 to 1.5 million years ago mark a new stage in hominin evolution. A number of paleoanthropologists recognize these fossils as those of a distinct species, *Homo ergaster*. *Homo ergaster* had a substantially larger brain than

H. habilis (over 900 cm^3), as well as long, slender legs with hip joints well adapted for long-distance walking **(Figure 34.50)**. The fingers were relatively short and straight, suggesting that *H. ergaster* did not climb trees like earlier hominins. *Homo ergaster* fossils have been discovered in far more arid environments than earlier hominins and have been associated with more sophisticated stone tools. Its smaller teeth also suggest that *H. ergaster* either ate different foods than australopiths (more meat and less plant material) or prepared some of its food before chewing, perhaps by cooking or mashing the food.



▲ Figure 34.50 Fossil of *Homo ergaster*. This 1.7-million-year-old fossil from Kenya belongs to a young *Homo ergaster* male. This individual was tall, slender, and fully bipedal, and he had a relatively large brain.

Homo ergaster marks an important shift in the relative sizes of the sexes. In primates, a size difference between males and females is a major component of sexual dimorphism (see Concept 23.4). On average, male gorillas and orangutans weigh about twice as much as females of their species. In *Australopithecus afarensis*, males were 1.5 times as heavy as females. The extent of sexual dimorphism decreased further in early *Homo*, a trend that continues through our own species: Human males weigh only about 1.2 times as much as females.

The reduced sexual dimorphism may offer some clues to the social systems of extinct hominins. In extant primates, extreme sexual dimorphism is associated with intense male-male competition for multiple females. In species that undergo more pair-bonding (including our own), sexual dimorphism is less dramatic. In *H. ergaster*, therefore, males and females may have engaged in more pair-bonding than earlier hominins did.

Fossils now generally recognized as *H. ergaster* once were considered early members of another species, *Homo erectus*, and some paleoanthropologists still hold this position. *Homo erectus* originated in Africa and was the first hominin to migrate out of Africa. The oldest fossils of hominins outside Africa, dating back 1.8 million years, were discovered in the present-day country of Georgia. *Homo erectus* eventually migrated as far as the Indonesian archipelago. Fossil evidence indicates that *H. erectus* became extinct between 200,000 and 70,000 years ago.

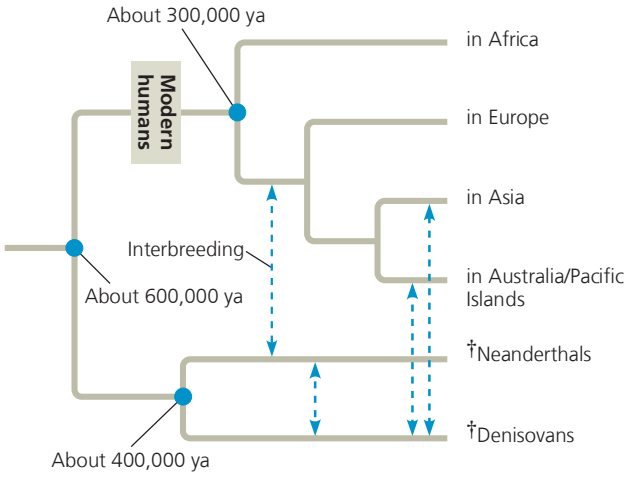
Neanderthals

In 1856, miners discovered some mysterious human fossils in a cave in the Neander Valley in Germany. The 40,000-year-old fossils belonged to a thick-boned hominin with a prominent brow. The hominin was named *Homo neanderthalensis* and is commonly called a Neanderthal. Neanderthals were living in Europe by 350,000 years ago and later spread to the Near East, central Asia, and southern Siberia. They had a brain larger than that of present-day humans, buried their dead, and made hunting tools from stone and wood. But despite their adaptations and culture, Neanderthals became extinct at some point between 28,000 and 40,000 years ago.

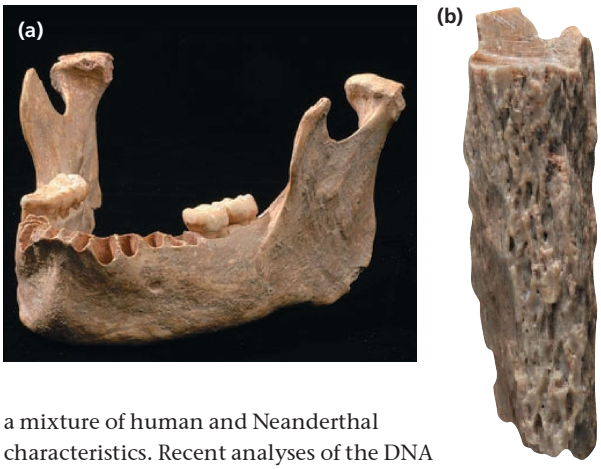
What is the evolutionary relationship of Neanderthals to *Homo sapiens*? Genetic data indicate that the lineages leading to *H. sapiens* and to Neanderthals diverged about 600,000 years ago **(Figure 34.51)**. This indicates that while Neanderthals and humans share a relatively recent common ancestor, humans did not descend directly from Neanderthals (as was once thought). Neanderthals were, in fact, more closely related to the "Denisovans," a hominin whose fossils have been discovered in Siberia and Tibet, than to humans.

Another long-standing question is whether mating occurred between Neanderthals and humans, leading to interspecific gene flow. Some researchers have argued that evidence of gene flow can be found in fossils that show

▼ Figure 34.51 Evolutionary relationships and interbreeding among humans, Neanderthals, and Denisovans. Genomic data and fossil evidence (see Figure 34.52) document multiple examples of interbreeding among humans, Neanderthals, and Denisovans.



▼ Figure 34.52 Fossil evidence of interbreeding among hominin species. (a) This jawbone belonged to a human who lived 40,000 years ago and had a relatively recent Neanderthal ancestor. **(b)** This bone fragment came from a woman who had a Neanderthal mother and a Denisovan father.



a mixture of human and Neanderthal characteristics. Recent analyses of the DNA sequence of the Neanderthal genome indicated that limited gene flow did occur between the two species. In 2015, the most extensive evidence yet of such gene flow was reported: DNA extracted from the fossil of a human jawbone was found to contain long stretches of Neanderthal DNA **(Figure 34.52a)**. In fact, the amount of Neanderthal DNA in this fossil indicated that this individual's great-great-great-grandparent was a Neanderthal.

Other recent genomic studies have shown that gene flow also occurred between Neanderthals and the Denisovans, whose DNA was isolated from bone fragments discovered in a Siberian cave. In 2018, for example, DNA analyses revealed that the 90,000-year-old bone fragment shown in **Figure 34.52b** came from a woman who had a Neanderthal mother and a Denisovan father—a remarkable discovery documenting the direct offspring of two different species of hominins. Genomic analyses also indicate that gene flow occurred between the Denisovans and our own species, *H. sapiens*.

Homo sapiens

Evidence from fossils, archaeology, and DNA studies has improved our understanding about how our own species, *Homo sapiens*, emerged and spread around the world.

Fossil evidence indicates that the ancestors of humans originated in Africa. Older species gave rise to later species, ultimately including *H. sapiens*. A 2017 study indicates that by 315,000 years ago, some hominin populations in Morocco had facial features like those of our species, while the back of the skull remained elongated, as in earlier species. The oldest known fossils of our species include specimens from Ethiopia that are 195,000 and 160,000 years old **(Figure 34.53)**. These early humans had less pronounced browridges than those found in *H. erectus* and Neanderthals, and they were more slender than other recent hominins. The Ethiopian fossils support inferences about the origin of humans from molecular evidence. DNA analyses show that Europeans and Asians share a relatively recent common ancestor and that many African lineages branched off more basal positions on the human family tree. These findings suggest that all living humans have ancestors that originated as *H. sapiens* in Africa.

▼ Figure 34.53 A 160,000-year-old-fossil of *Homo sapiens*.



The oldest fossils of *H. sapiens* outside Africa are from the Middle East and date back about 180,000 years. Fossil evidence and genetic analyses suggest that humans spread beyond Africa in one or more waves, first into Asia and then to Europe and Australia. The date of the first arrival of humans in the New World is uncertain, although the oldest generally accepted evidence puts that date at about 15,000 years ago.

New findings continually update our understanding of the human evolutionary lineage. For example, in 2015, the human family gained a new member, *Homo naledi*. The structure of its foot indicates that *H. naledi* was fully bipedal, and the shape of its hand suggests that *H. naledi* had fine motor skills **(Figure 34.54)**, as in *H. sapiens*, Neanderthals, and other species that used tools extensively. But *H. naledi* also had a small brain, a broadly flared upper pelvis, and other features that have led researchers to conclude that it was an early member of our genus.

As an early member of our genus, it is likely that *H. naledi* originated more than 1.5 million years ago—yet initial estimates of the age of the *H. naledi* fossils ranged from 3 million

▼ Figure 34.54 Fossils of hand bones and foot bones (top and side views) of *Homo naledi*.



years old to just 100,000 years old. Scientists didn't know how old the fossils are because they were found on the floor of a deep cave, not encased in rocks that could be dated using radioactive isotopes. In 2017, however, teeth from a newly discovered *H. naledi* skull were dated using radioactive isotopes and found to be 300,000 years old. Overall, fossil evidence suggests that *H. naledi* arose 1–2 million years ago (like other early members of our genus) and then persisted almost until the present.

About ten years before the discovery of *H. naledi*, researchers reported another astonishing find: skeletal remains of adult hominins dating from 100,000 to 60,000 years ago and representing a previously unknown species, *Homo floresiensis*. First discovered in a limestone cave on the Indonesian island of Flores, the individuals were much shorter and had a much smaller brain volume than *H. sapiens*—more similar, in fact, to an australopith. The researchers who discovered these fossils argue that certain features of the skeletons, such as the shape of the teeth and the thickness and proportions of the skull, suggest that *H. floresiensis* descended from the larger *H. erectus*. Not convinced, some researchers have argued that the fossils represent small *H. sapiens* individuals with a disorder such as Down syndrome or microcephaly (a condition in which a person has a deformed, miniature brain).

Over the past few years, most studies have supported the designation of *H. floresiensis* as a new hominin. One such study found that the wrist bones of the Flores fossils are similar in shape to those of nonhuman apes and early hominins, but different from those of Neanderthals and *H. sapiens*. These researchers concluded that the Flores fossils represent a species whose lineage branched off before the origin of the clade that includes Neanderthals and humans. A different study comparing the foot bones of the Flores fossils with those of other hominins also concluded that *H. floresiensis* arose before *H. sapiens*. Finally, in 2016, *H. floresiensis*-like fossils dating to 700,000 years ago were discovered at a second location on Flores—again indicating that the *H. floresiensis* lineage branched off long before the origin of *H. sapiens*. Open questions that may yet be answered by new discoveries include how *H. floresiensis* originated and whether it survived long enough to encounter *H. sapiens*, which was living in Indonesia by 50,000 years ago.

The rapid expansion of our species may have been spurred by changes in human cognition as *H. sapiens* evolved in Africa. Evidence of sophisticated thought in *H. sapiens* includes the recent discovery in South Africa of 77,000-year-old art—geometric markings made on pieces of ochre **(Figure 34.55)**. Similarly, archaeologists working in southern and eastern Africa recently found 75,000-year-old ostrich eggs and snail shells with holes neatly drilled through them. By 30,000 years ago, humans were producing spectacular cave paintings.

While these developments can help us understand the spread of *H. sapiens*, it is not clear whether they played a role in the extinction of other hominins. Neanderthals, for example, also made complex tools and showed a capacity for symbolic thought. As a result, while some scientists have suggested that Neanderthals were driven to extinction by competition with *H. sapiens*, others question that idea.

▼ Figure 34.55 Art, a human hallmark. The engravings on this 77,000-year-old piece of ochre, discovered in South Africa's Blombos Cave, are among the earliest signs of symbolic thought in humans.



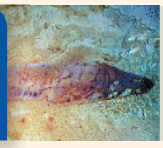
Our discussion of humans brings this unit on biological diversity to an end. But keep in mind that our sequence of topics isn't meant to imply that life consists of a ladder leading from lowly microorganisms to lofty humanity. Biological diversity is the product of branching phylogeny, not ladderlike "progress." The fact that there are almost as many species of ray-finned fishes alive today as in all other vertebrate groups combined shows that our finned relatives are not outmoded underachievers that failed to leave the water. The tetrapods—amphibians, reptiles, and mammals—are derived from one lineage of lobe-finned vertebrates. As tetrapods diversified on land, fishes continued their branching evolution in the greatest portion of the biosphere's volume. Similarly, the ubiquity of diverse prokaryotes throughout the biosphere today is a reminder of the enduring ability of these relatively simple organisms to keep up with the times through adaptive evolution. Biology exalts life's diversity, past and present.

CONCEPT CHECK 34.7

1. Identify some characters that distinguish hominins from other apes.
2. Provide an example in which different features of organisms in the hominin evolutionary lineage evolved at different rates.
3. **WHAT IF?** Some genetic studies suggest that the most recent common ancestor of *Homo sapiens* that lived outside of Africa left Africa about 50,000 years ago. Compare this date with the dates of fossils given in the text. Can both the genetic results and the dates ascribed to the fossils be correct? Explain.

For suggested answers, see Appendix A.

34 Chapter Review



Go to **Mastering Biology** for Assignments, the eText, the Study Area, and Dynamic Study Modules.

SUMMARY OF KEY CONCEPTS

To review key terms, go to the **Vocabulary Self-Quiz** in the **Mastering Biology** eText or Study Area, or go to goo.gl/zkjz9t.

Key Concept	Clade	Description
CONCEPT 34.1 **Chordates have a notochord and a dorsal, hollow nerve cord** *(pp. 719–722)* ? *Describe likely features of the common ancestor of chordates. Explain your answer.*	Cephalochordata (lancelets)	Basal chordates; marine suspension feeders that exhibit four key derived characters of chordates
	Urochordata (tunicates)	Marine suspension feeders; larvae display the derived traits of chordates
CONCEPT 34.2 **Vertebrates are chordates that have a backbone** *(pp. 722–725)* ? *Identify the shared features of early fossil vertebrates.*	Myxini (hagfishes) and Petromyzontida (lampreys)	Jawless aquatic vertebrates with reduced vertebrae; hagfishes have a head with a skull and brain, eyes, and other sensory organs; some lampreys feed by attaching to a live fish and ingesting its blood
CONCEPT 34.3 **Gnathostomes are vertebrates that have jaws** *(pp. 725–730)* ? *How would the appearance of organisms with jaws have altered ecological interactions? Provide supporting evidence.*	Chondrichthyes (sharks, rays, skates, ratfishes)	Aquatic gnathostomes; have a cartilaginous skeleton, a derived trait formed by the reduction of an ancestral mineralized skeleton
	Actinopterygii (ray-finned fishes)	Aquatic gnathostomes; have a bony skeleton and maneuverable fins supported by rays
	Actinistia (coelacanths)	Ancient lineage of aquatic lobe-fins still surviving in Indian Ocean
	Dipnoi (lungfishes)	Freshwater lobe-fins with both lungs and gills; sister group of tetrapods
CONCEPT 34.4 **Tetrapods are gnathostomes that have limbs** *(pp. 730–734)* ? *Which features of amphibians restrict most species to living in aquatic or moist terrestrial habitats?*	Amphibia (salamanders, frogs, caecilians)	Have four limbs descended from modified fins; most have moist skin that functions in gas exchange; many live both in water (as larvae) and on land (as adults)
CONCEPT 34.5 **Amniotes are tetrapods that have a terrestrially adapted egg** *(pp. 734–741)* ? *Explain why birds are considered reptiles.*	Reptilia (tuataras, lizards and snakes, turtles, crocodilians, birds)	One of two groups of living amniotes; have amniotic eggs and rib cage ventilation, key adaptations for life on land
CONCEPT 34.6 **Mammals are amniotes that have hair and produce milk** *(pp. 741–747)* ? *Describe the origin and early evolution of mammals.*	Mammalia (monotremes, marsupials, eutherians)	Evolved from synapsid ancestors; include egg-laying monotremes (echidnas, platypus); pouched marsupials (such as kangaroos, opossums); and eutherians (placental mammals, such as rodents, primates)

Chordates: notochord; dorsal, hollow nerve cord; pharyngeal slits; post-anal tail

Vertebrates: *Hox* genes duplication, backbone of vertebrae

Cyclostomes: jawless vertebrates

Gnathostomes: hinged jaws, four sets of *Hox* genes

Osteichthyans: bony skeleton

Lobe-fins: muscular fins or limbs

Tetrapods: four limbs, neck, fused pelvic girdle

Amniotes: amniotic egg, rib cage ventilation

CONCEPT 34.7

Humans are mammals that have a large brain and bipedal locomotion *(pp. 748–754)*

- Derived characters of humans include bipedalism and a larger brain and reduced jaw compared with other apes.
- **Hominins**—humans and species that are more closely related to humans than to chimpanzees—originated in Africa about 8 million years ago. Early hominins had a small brain but probably walked upright.
- The oldest evidence of tool use is 2.5 million years old.
- *Homo ergaster* was the first fully bipedal, large-brained hominin. *Homo erectus* was the first hominin to leave Africa.
- Neanderthals lived in Europe and the Near East from about 350,000 to 28,000 years ago.
- *Homo sapiens* originated in Africa about 195,000 years ago and began to spread to other continents about 180,000 years ago.

? *Based on fossil evidence, summarize how key hominin features have changed over time.*

TEST YOUR UNDERSTANDING

For more multiple-choice questions, go to the **Practice Test** in the **Mastering Biology** eText or Study Area, or go to goo.gl/GruWRg.

Levels 1-2: Remembering/Understanding

1. Vertebrates and tunicates share
   (A) jaws adapted for feeding.
   (B) a high degree of cephalization.
   (C) an endoskeleton that includes a skull.
   (D) a notochord and a dorsal, hollow nerve cord.
2. Living vertebrates can be divided into two major clades. Select the appropriate pair.
   (A) the chordates and the tetrapods
   (B) the urochordates and the cephalochordates
   (C) the cyclostomes and the gnathostomes
   (D) the marsupials and the eutherians
3. Unlike eutherians, *both* monotremes and marsupials
   (A) lack nipples.
   (B) have some embryonic development outside the uterus.
   (C) lay eggs.
   (D) are found in Australia and Africa.
4. In Figure 34.25, which of the following is the sister taxon to the archosaurs?
   (A) synapsids (C) turtles
   (B) crocodilians (D) lepidosaurs
5. As hominins diverged from other primates, which of the following appeared first?
   (A) reduced jawbones (C) the making of stone tools
   (B) an enlarged brain (D) bipedal locomotion

Levels 3-4: Applying/Analyzing

6. Which of the following could be considered the most recent common ancestor of living tetrapods?
   (A) a sturdy-finned, shallow-water lobe-fin whose appendages had skeletal supports similar to those of terrestrial vertebrates
   (B) an armored, jawed placoderm with two pairs of appendages
   (C) an early ray-finned fish that developed bony skeletal supports in its paired fins
   (D) a salamander that had legs supported by a bony skeleton but moved with the side-to-side bending typical of fishes
7. **EVOLUTION CONNECTION** Living members of a vertebrate lineage can be very different from early members of the lineage, and evolutionary reversals (character losses) are common. Give examples that illustrate these observations, and explain their evolutionary causes.

Levels 5-6: Evaluating/Creating

8. **SCIENTIFIC INQUIRY • DRAW IT** As a consequence of size alone, larger organisms tend to have larger brains than smaller organisms. However, some organisms have brains that are considerably larger than expected for their size. There are high energetic costs associated with the development and maintenance of brains that are large relative to body size.
   (a) The fossil record documents trends in which brains that are large relative to body size evolved in certain lineages, including hominins. In such lineages, what can you infer about the costs and benefits of large brains?
   (b) Hypothesize how natural selection might favor the evolution of large brains despite their high maintenance costs.
   (c) Data for 14 bird species are listed below. Graph the data, placing deviation from expected brain size on the *x*-axis and mortality rate on the *y*-axis. What can you conclude about the relationship between brain size and mortality?

Deviation from Expected Brain Size*	−2.4	−2.1	−2.0	−1.8	−1.0	0.0	0.3	0.7	1.2	1.3	2.0	2.3	3.0	3.2
Mortality Rate	0.9	0.7	0.5	0.9	0.4	0.7	0.8	0.4	0.8	0.3	0.6	0.6	0.3	0.6

Data from D. Sol et al., Big-brained birds survive better in nature, *Proceedings of the Royal Society B* 274:763–769 (2007).

*Values < 0 indicate brain sizes smaller than expected; values > 0 indicate sizes larger than expected.

9. **WRITE ABOUT A THEME: ORGANIZATION** Early tetrapods had a sprawling gait (like that of a lizard): As the right front foot moved forward, the body twisted to the left and the left rib cage and lung were compressed; the reverse occurred with the next step. Normal breathing, in which both lungs expand equally with each breath, was hindered during walking and prevented during running. In a short essay (100–150 words), explain how the origin of organisms such as dinosaurs, whose gait allowed them to move without compressing their lungs, could have led to emergent properties.
10. **SYNTHESIZE YOUR KNOWLEDGE**



This animal is a vertebrate with hair. What can you infer about its phylogeny? Identify as many key derived characters as you can that distinguish this animal from invertebrate chordates.

For selected answers, see Appendix A.