24 Early Life and the Diversification of Prokaryotes

KEY CONCEPTS

24.1 Conditions on early Earth made the origin of life possible
24.2 Diverse structural and metabolic adaptations have evolved in prokaryotes
24.3 Rapid reproduction, mutation, and genetic recombination promote genetic diversity in prokaryotes
24.4 Prokaryotes have radiated into a diverse set of lineages
24.5 Prokaryotes play crucial roles in the biosphere

▼ **Figure 24.1** What organisms lived on early Earth?

OVERVIEW

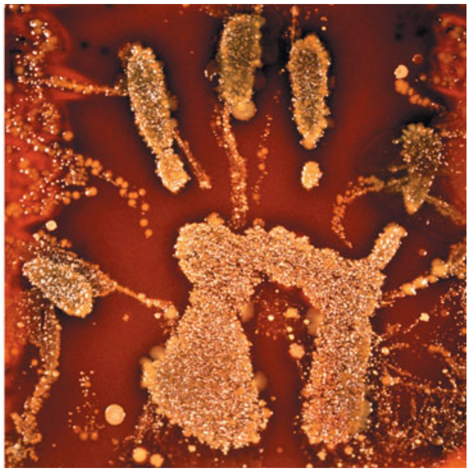
The First Cells

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 birth 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. As a result, life probably could not have originated or survived during this time.

This massive bombardment ended about 4 billion years ago, setting the stage for the origin of life on our young planet. While chemical signatures of life date back to 3.8 billion years ago, the earliest direct evidence comes from fossils that are 3.5 billion years old. These fossils are of **prokaryotes**, an informal term for single-celled organisms in domains Bacteria and Archaea (see Figure 20.20). Some of the earliest prokaryotic cells lived in dense mats similar to those that resemble stepping stones in **Figure 24.1**; others lived as free-floating, individual cells. These early prokaryotes were Earth's first organisms, and their descendants had the planet to themselves for about 1.5 billion years—until eukaryotes first appeared about 1.8 billion years ago (see Concept 25.1).

Over their long evolutionary history, descendants of Earth's first cells have given rise to the vast diversity of prokaryotes living today. This diversity includes "extreme" species such as *Deinococcus radiodurans*, which can survive 3 million rads of radiation (3,000 times the dose fatal to humans). Other prokaryotes live in environments that are too cold or hot or salty for most other organisms, and some have even been found living in rocks 3.2 km (2 miles) below Earth's surface.

But prokaryotic species also thrive in more "normal" habitats—the lands and waters in which most other species are found. And within these lands and waters, prokaryotes have colonized the bodies of other organisms that live there, including humans **(Figure 24.2)**. Their ability to live in 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 origin, adaptations, diversity, and enormous ecological impact of these remarkable organisms.



▶ **Figure 24.2 Bacteria that inhabit the human body.** Touching an agar gel led to the handprint-shaped growth of *Staphylococcus epidermidis*, just one of more than 1,000 species of bacteria that live on or in the human body.

CONCEPT 24.1

Conditions on early Earth made the origin of life possible

The earliest fossils are of prokaryotes 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.

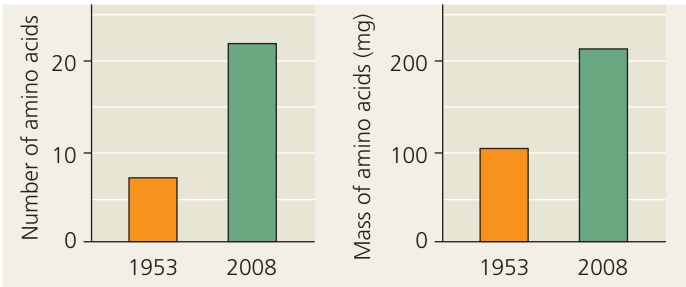
Synthesis of Organic Compounds on Early Earth

As the bombardment of early Earth ended, the first atmosphere had little oxygen and was probably thick with water vapor, along with compounds released by volcanic eruptions, including 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 organic synthesis could have come from lightning and intense 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 under the guidance of 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. 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 or deep-sea vents, where hot water and minerals gush into the ocean from Earth's interior. In a 2008 test of the volcanic-atmosphere hypothesis, researchers used modern equipment to reanalyze molecules that Miller had saved from one of his experiments. The study found that numerous amino acids had formed under conditions that simulated a volcanic eruption **(Figure 24.3)**.



▲ **Figure 24.3 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 original 1953 experiment.

MAKE CONNECTIONS *After reviewing Concept 3.5, explain how more than 20 amino acids could have been produced in the 2008 experiment.*

Miller-Urey-type experiments show that the abiotic synthesis of organic molecules is possible under various assumptions about the composition of the early atmosphere. A second source of organic molecules may have been meteorites. For example, fragments of the Murchison meteorite, a 4.5-billion-year-old rock that fell to Australia in 1969, contain more than 80 amino acids, some in large amounts. These amino acids cannot be contaminants from Earth because they include an equal mix of two different structural forms—only one of which is typically produced or used by organisms on our planet. Recent 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

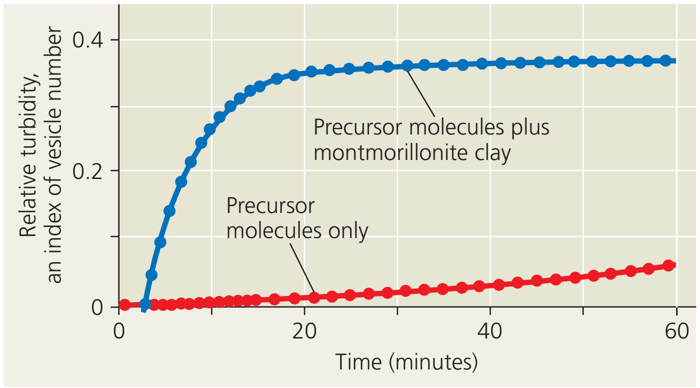
The presence of small organic molecules, such as amino acids and nitrogenous bases, is not sufficient for the emergence of life as we know it. Every cell has a vast assortment of macromolecules, including enzymes and other proteins and the nucleic acids that are essential for self-replication. Could such macromolecules have formed on early Earth? A 2009 study demonstrated that one key step, the abiotic synthesis of RNA monomers, can occur spontaneously from simple precursor molecules. 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. Nevertheless, it is possible that such polymers may have acted as weak catalysts for a variety of chemical reactions on early Earth.

Protocells

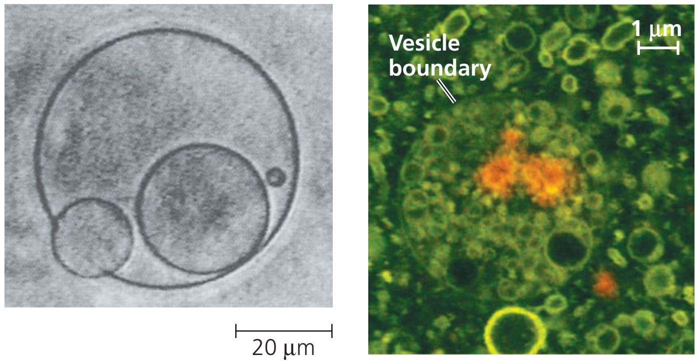
All organisms must be able to carry out reproduction and energy processing (metabolism). Life cannot persist without both of these functions. DNA molecules carry genetic information, including the instructions needed to replicate themselves accurately during reproduction. But the replication of DNA requires elaborate enzymatic machinery, along with an abundant supply of nucleotide building blocks that are provided by the cell's metabolism (see Chapter 13). This suggests that self-replicating molecules and a metabolism-like source of the building blocks may have appeared together in early protocells. How did that happen?

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.

For example, vesicles can form spontaneously when lipids or other organic molecules are added to water. When this



(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).

▲ **Figure 24.4 Features of abiotically produced vesicles.**

occurs, the hydrophobic molecules in the mixture 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 **(Figure 24.4a)**. 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 **(Figure 24.4b)**, 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 **(Figure 24.4c)**. 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.

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 perform many enzyme-like catalytic functions (see Chapter 14). Such RNA catalysts are called **ribozymes**.

Some ribozymes can make complementary copies of short pieces of RNA, if 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 particular environment, RNA molecules with certain nucleotide sequences replicate faster and with fewer errors than other sequences. The RNA molecule whose sequence is best suited to the surrounding environment and has the greatest ability to replicate itself will leave the most descendant molecules. Occasionally, a copying error will result in a molecule that folds into a shape that is more adept at self-replication than the ancestral sequence. 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 could replicate and store genetic information about the vesicles that carried them.

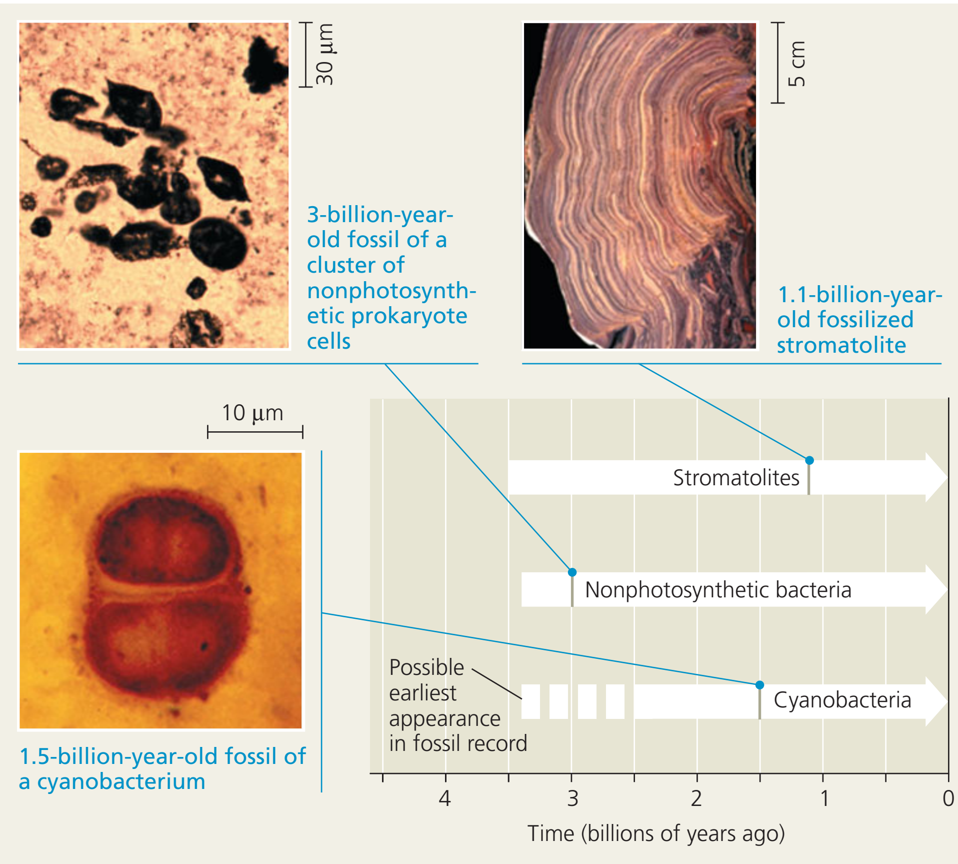
A vesicle with self-replicating, catalytic RNA would differ from its many neighbors that lacked such molecules. If that vesicle could grow, split, and pass its RNA molecules to its daughters, the daughters would be protocells that had some of the properties of their parent. Although the first such protocells 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.

Fossil Evidence of Early Life

Many of the oldest known fossils are of *stromatolites*, layered rocks that form from the activities of certain prokaryotes **(Figure 24.5)**. The earliest stromatolites date to 3.5 billion years ago. For several hundred million years, all such fossils were similar in overall structure and all were from shallow marine bays; stromatolites are still found in such bays today (see Figure 23.2). By 3.1 billion years ago, stromatolites with two distinctly different morphologies had appeared, and by 2.8 billion years ago, stromatolites occurred in salty lakes as well as marine environments. Thus, early fossil stromatolites show signs of ecological and evolutionary change over time.

Ancient fossils of individual prokaryotic cells have also been discovered that are nearly as old as the oldest stromatolites. For example, a 2011 study found fossilized prokaryotic cells in 3.4-billion-year-old rocks from Australia (see Figure 24.5). In South Africa, other researchers have found 3.4-billion-year-old fossils of prokaryotes that resemble cyanobacteria, a group of photosynthetic bacteria living today. Some scientists question whether the South African fossils really were cyanobacteria, but by 2.5 billion years ago, diverse communities of cyanobacteria lived in the oceans. Cyanobacteria remained the main photosynthetic organisms for over a billion years, and they continue to be one of the most important groups of photosynthetic organisms alive today.



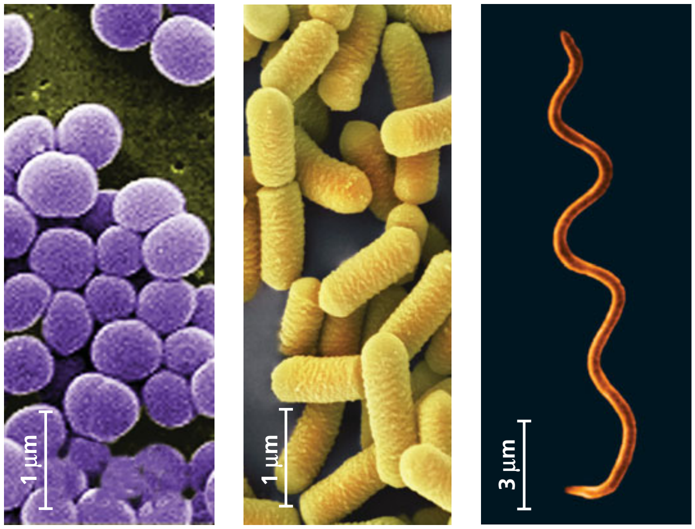
▲ **Figure 24.5 Appearance in the fossil record of early prokaryote groups.**

Early cyanobacteria began what is arguably the greatest impact organisms have ever had on our planet: the release of oxygen to Earth's atmosphere during the water-splitting step of photosynthesis. In certain 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. As we'll see, 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.

CONCEPT CHECK 24.1

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. Summarize fossil evidence of early prokaryotes. Describe how these organisms altered Earth's atmosphere.
4. **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 14.4 and 17.7, suggest how this could have occurred. Is such a flow a common occurrence today?

For suggested answers, see Appendix A.



(a) Spherical **(b) Rod-shaped** **(c) Spiral**

▲ **Figure 24.6 The most common shapes of prokaryotes.**
(a) Cocci (singular, *coccus*) are spherical prokaryotes. They occur singly, in pairs (diplococci), in chains of many cells (streptococci), and in clusters resembling bunches of grapes (staphylococci). **(b)** Bacilli (singular, *bacillus*) are rod-shaped prokaryotes. They are usually solitary, but in some forms the rods are arranged in chains (streptobacilli). **(c)** Spiral prokaryotes include spirilla, which range from comma-like shapes to loose coils, and spirochetes (shown here), which are corkscrew-shaped (colorized SEMs).

CONCEPT 24.2

Diverse structural and metabolic adaptations have evolved in prokaryotes

Throughout their long history, prokaryotic populations have been (and continue to be) subjected to natural selection in all kinds of environments, resulting in their enormous diversity today. As described in Concept 24.1, fossils of early prokaryotes document some of the major steps in their evolutionary history, including the appearance of the first photosynthetic organisms. However, prokaryotic populations have also evolved in ways that cannot be seen in the fossil record, including changes in the type and efficiency of their enzymes. Although we cannot trace the time course of such changes in the fossil record, we can examine their end results—the adaptations found in prokaryotes today. We'll survey those adaptations here, beginning with a description of prokaryotic cells.

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 10–100 µm diameter of many eukaryotic cells. (One notable exception, *Thiomargarita namibiensis*, can be as large as 750 µm in diameter—bigger than the dot on this i.) Prokaryotic cells have a variety of shapes **(Figure 24.6)**. 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

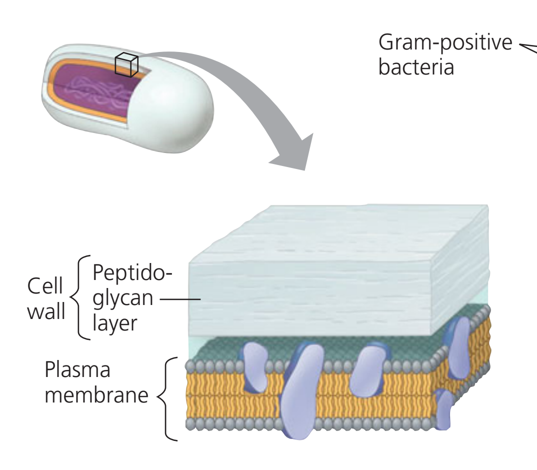
A key feature of nearly all prokaryotic cells is the cell wall, which maintains cell shape, protects the cell, and prevents it from bursting in a hypotonic environment (see Concept 5.3). In a hypertonic environment, most prokaryotes lose water and shrink away from their wall (plasmolyze). Such water 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 rapidly multiplying.

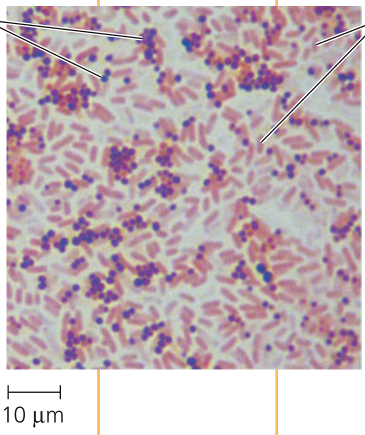
The cell walls of prokaryotes differ in structure from those of eukaryotes. In eukaryotes that have cell walls, such as plants and fungi, the walls are usually made of cellulose or chitin (see Concept 3.3). In contrast, most bacterial cell walls contain **peptidoglycan**, a polymer composed of modified 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 staining technique developed by the Dutch scientist Hans Christian Gram, biologists can categorize many bacterial species according to cell wall composition **(Figure 24.7)**. **Gram-positive** bacteria have simpler walls with a relatively large amount of peptidoglycan. **Gram-negative** bacteria have less peptidoglycan and are structurally more complex, with an outer membrane that contains lipopolysaccharides

▼ **Figure 24.7 Gram staining.**

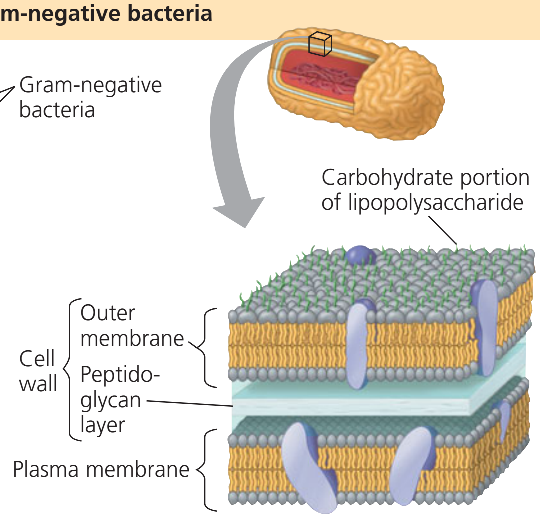
(a) Gram-positive bacteria





Gram-positive bacteria stain a darker color and have a thick cell wall made of peptidoglycan.

(b) Gram-negative bacteria



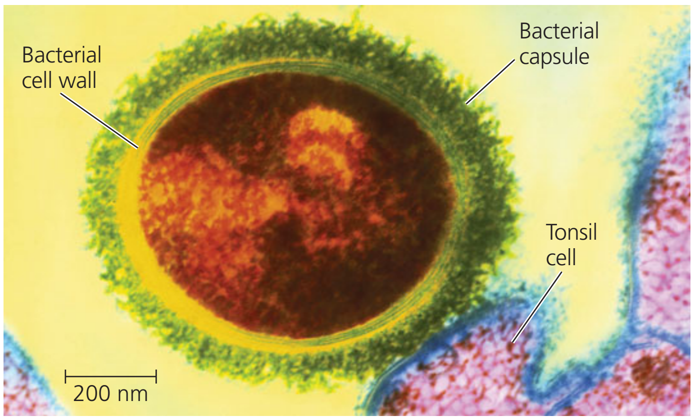
Gram-negative bacteria have a thinner layer of peptidoglycan located between the plasma membrane and an outer membrane.

(carbohydrates bonded to lipids). These differences in cell wall composition have medical 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 entry of the drugs.

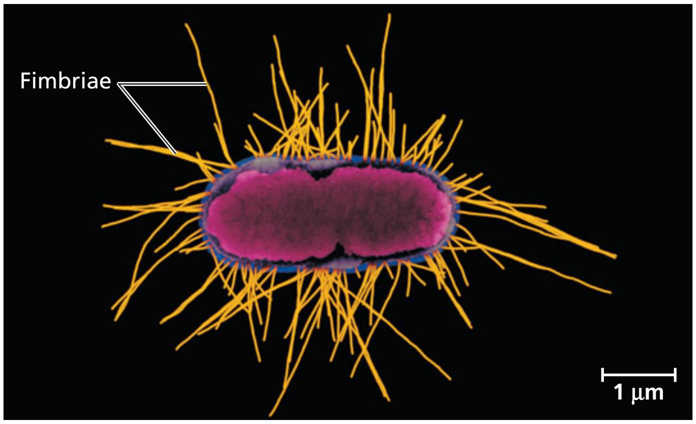
The cell wall of many prokaryotes is surrounded by a sticky layer of polysaccharide or protein. This layer is called a **capsule** if it is dense and well defined **(Figure 24.8)** or a *slime layer* if it is not as well organized. Both kinds of sticky outer layers enable prokaryotes to adhere to their substrate or to other individuals in a colony. Some capsules and slime layers protect against dehydration, and some shield pathogenic prokaryotes from attacks by their host's immune system.

Other bacteria develop resistant cells called **endospores** when they lack an essential nutrient. The original cell produces a copy of its chromosome and surrounds that copy with a tough multilayered structure, forming the endospore. Water is removed from the endospore, halting its metabolism, and 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** (singular, *fimbria*) **(Figure 24.9)**. For example, the bacterium that causes gonorrhea, *Neisseria gonorrhoeae*, uses fimbriae to fasten itself to the mucous membranes of its host. Fimbriae are usually



▲ **Figure 24.8 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.



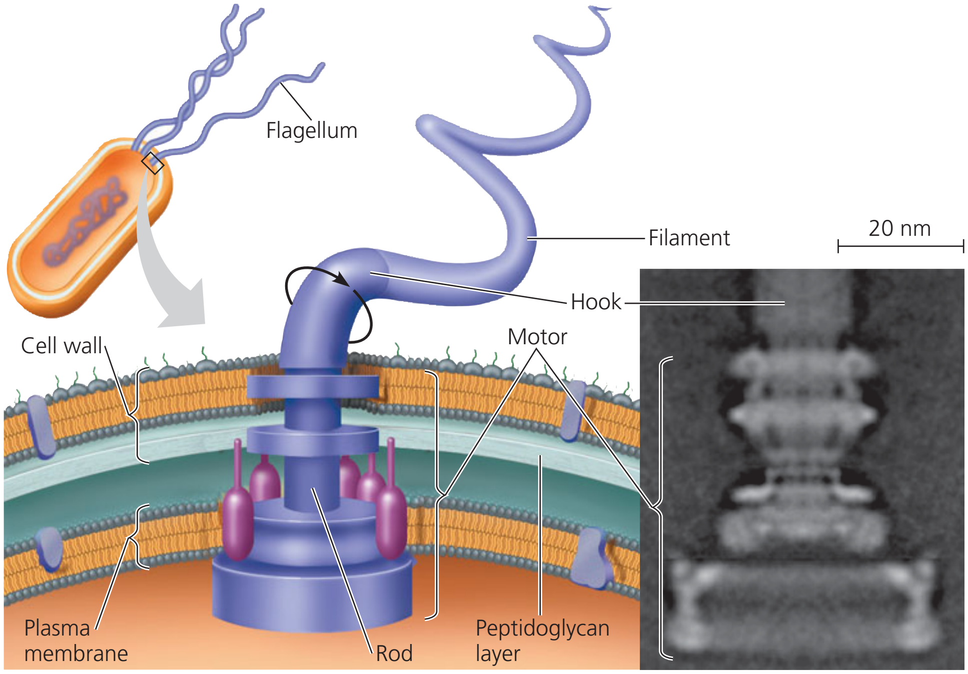
▲ **Figure 24.9 Fimbriae.** These numerous protein-containing appendages enable some prokaryotes to attach to surfaces or to other cells (colorized TEM).

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 24.16); 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 24.10)**. 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 4.23). 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 propulsion 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.



▲ **Figure 24.10 A prokaryotic flagellum.** The motor of a prokaryotic flagellum consists of a system of rings embedded in the cell wall and plasma membrane (TEM). ATP-driven pumps in the membrane transport 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.)

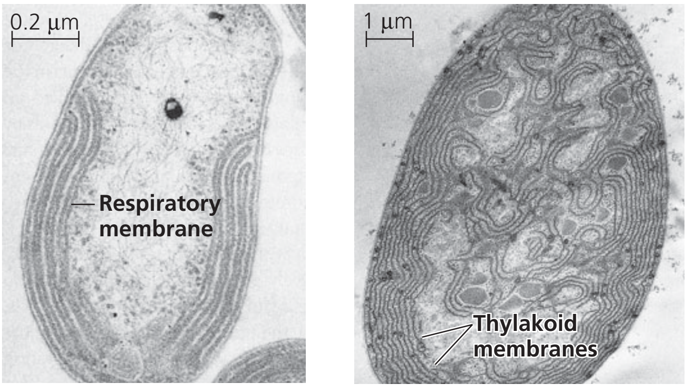
Evolutionary Origins of Bacterial Flagella

The bacterial flagellum shown in Figure 24.10 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 23.4), 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 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 are homologous to 10 similar proteins in a secretory system found in bacteria. (A secretory system is a protein complex that enables a cell to secrete 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 existing structures 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 4.4). 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 24.11)**. 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 (and that do not have a membrane).

The genome of a prokaryote is structurally different from a eukaryotic genome and in most cases has considerably less



(a) Aerobic prokaryote **(b) Photosynthetic prokaryote**

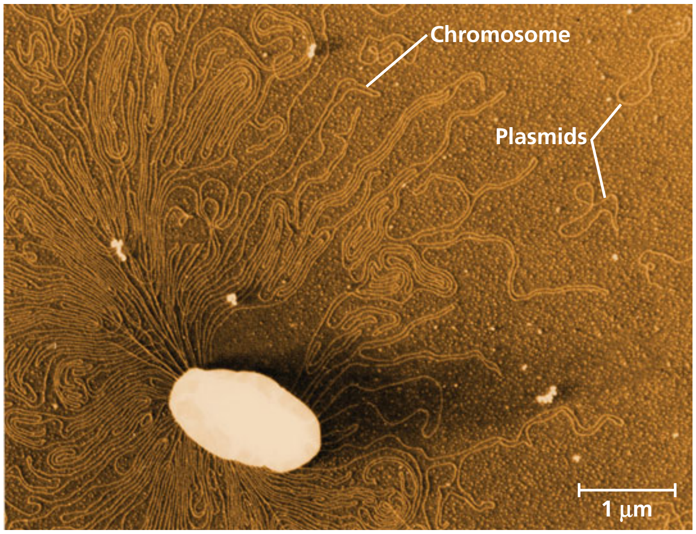
▲ **Figure 24.11 Specialized membranes of prokaryotes.** **(a)** Infoldings of the plasma membrane, reminiscent of the cristae of mitochondria, function in cellular respiration in some aerobic prokaryotes (TEM). **(b)** Photosynthetic prokaryotes called cyanobacteria have thylakoid membranes, much like those in chloroplasts (TEM).

DNA. Prokaryotes generally have circular chromosomes **(Figure 24.12)**, whereas eukaryotes have 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 24.12), 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 between the two groups (see Chapters 13 and 14). 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.

Nutritional and Metabolic Adaptations

Like all organisms, prokaryotes can be categorized by how they obtain energy and the carbon used in building organic molecules. 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.



▲ **Figure 24.12 A prokaryotic chromosome and plasmids.** The thin, tangled loops surrounding this ruptured *E. 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.

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 possible energy sources and carbon sources results in four major modes of nutrition, summarized in **Table 24.1**.

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 (see Chapter 7) 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

Table 24.1 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

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

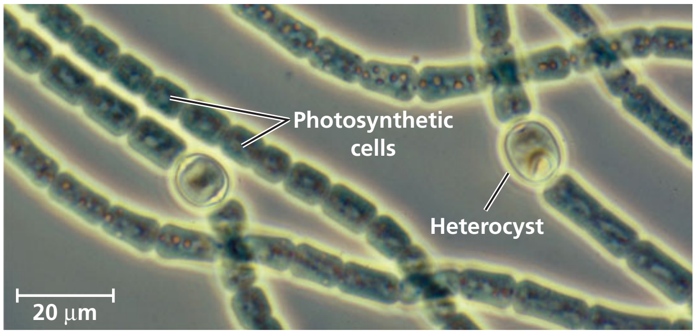
Nitrogen is essential for the production of amino acids and nucleic acids in all organisms. Whereas eukaryotes can obtain nitrogen from only a limited group of nitrogen compounds, prokaryotes can metabolize nitrogen in a wide variety of forms. For example, some cyanobacteria and some methanogens (a group of 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 their 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 by prokaryotes has a large impact on other organisms. For example, it can increase the nitrogen available to plants, which cannot use atmospheric nitrogen but can use the nitrogen compounds that the prokaryotes produce from ammonia. Chapter 42 discusses this and other essential roles of prokaryotes 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, but a single cell cannot carry out both processes at the same time. The reason is that photosynthesis produces O_2, which inactivates the enzymes involved in nitrogen fixation. Instead of living as isolated cells, *Anabaena* forms filamentous chains **(Figure 24.13)**. 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 between different 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. Channels in the biofilm allow nutrients to reach cells in the interior and wastes to be expelled. Biofilms are common in nature, but they can cause problems by contaminating industrial products and medical equipment and contributing to tooth decay and more serious health problems. Altogether, damage caused by biofilms costs billions of dollars annually.



▲ **Figure 24.13 Metabolic cooperation in a prokaryote.** In the filamentous cyanobacterium *Anabaena*, cells called heterocysts fix nitrogen, while the other cells carry out photosynthesis (LM). *Anabaena* is found in many freshwater lakes.

Reproduction

Many prokaryotes can reproduce quickly in favorable environments. By *binary fission* (see Figure 9.12), 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 fact that many prokaryotic species can divide after short periods of time draws attention to 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.

Adaptations of Prokaryotes: *A Summary*

Let's step back and examine the big picture of the adaptations that have arisen in prokaryotic populations. We've described some of their key structural features, such as cell walls, endospores, fimbriae, and flagella. But prokaryotic cells are much simpler structurally than are eukaryotic cells—they do not vary as much in shape or size, and they lack the complex compartmentalization associated with the membrane-enclosed organelles of eukaryotic cells. Indeed, the ongoing success of prokaryotes is not primarily a story of structural diversification; rather, their success is an extraordinary example of physiological and metabolic diversification. As we've seen, prokaryotes thrive under a wide variety of physical and chemical conditions, and they have an astonishing range of metabolic adaptations that allow them to obtain energy and carbon in these environments.

Overall, the metabolic diversification of prokaryotes can be viewed as a first great wave of adaptive radiation in the evolutionary history of life. Bearing that broad perspective in mind, we turn now to the genetic diversity that has enabled the adaptations found in prokaryotic populations.

CONCEPT CHECK 24.2

1. Contrast the cellular and DNA structures of prokaryotes and eukaryotes.
2. Distinguish between the four major modes of nutrition, noting which are unique to prokaryotes.
3. **MAKE CONNECTIONS** Suggest a hypothesis to explain why the thylakoid membranes of chloroplasts resemble those of cyanobacteria. Refer to Figures 4.16 and 20.20.
4. **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 24.3

Rapid reproduction, mutation, and genetic recombination promote genetic diversity in prokaryotes

As we saw in Unit Three, evolution cannot occur without genetic variation. The evolutionary changes seen in the prokaryotic fossil record and the diverse adaptations found in prokaryotes living today 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

The generation of a novel allele by a new mutation is rare for any particular gene. Moreover, since prokaryotes do not reproduce sexually, at first glance their extensive genetic variation may seem puzzling. But in many species, this variation can result from rapid reproduction and mutation.

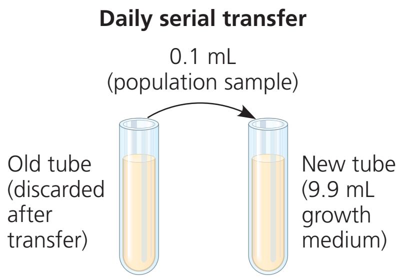
Consider the bacterium *Escherichia coli* as it reproduces by binary fission in a human intestine, one of its natural environments. After repeated rounds of division, most of the offspring cells are genetically identical to the original parent cell. However, if errors occur during DNA replication, some 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. Thus, the total number of mutations when all 4,300 *E. coli* genes are considered is about $4{,}300 \times 2{,}000 = 9$ 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: Individuals that are genetically better equipped for their environment tend to survive and reproduce at higher rates than other individuals **(Figure 24.14)**. The ability of prokaryotes to adapt rapidly to

▼ **Figure 24.14** **Inquiry**

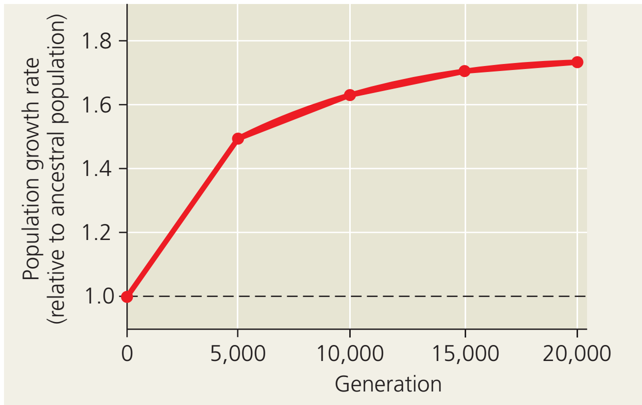
Can prokaryotes evolve rapidly in response to environmental change?

Experiment Vaughn Cooper and Richard Lenski 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 in their new environment, resulting in the rapid evolution of increased population growth rates.

Source 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.

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 over 3.5 billion years, prokaryotic populations have responded successfully to many different types of environmental challenges.

Genetic Recombination

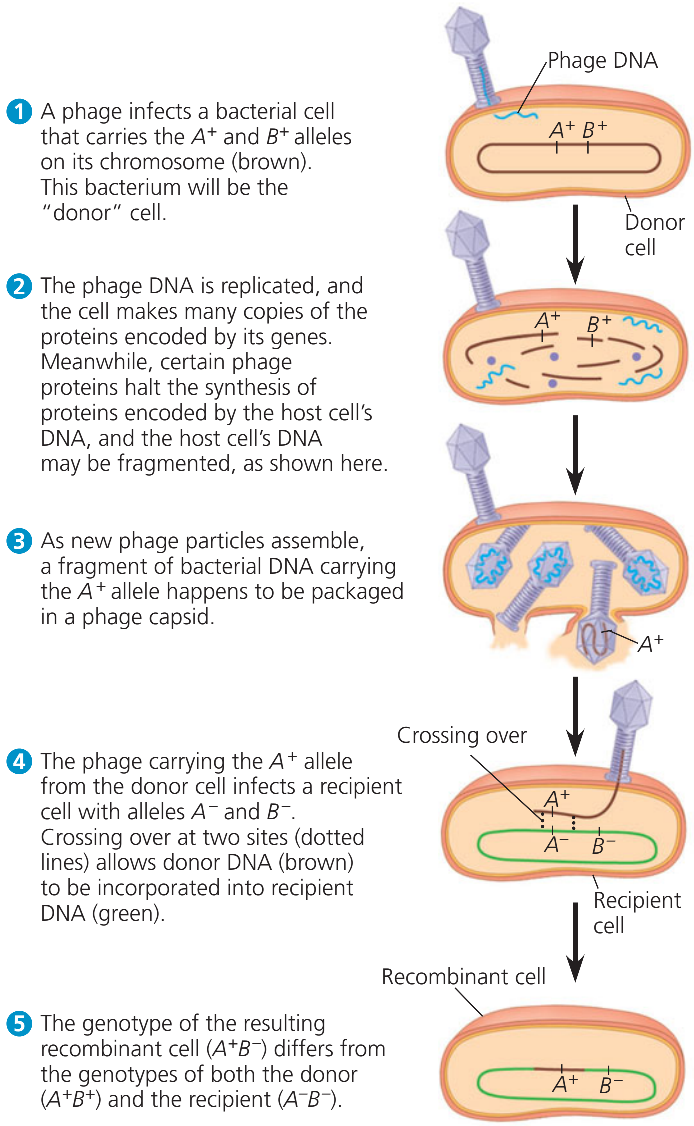
Although new mutations are a major source of variation in prokaryotic populations, additional diversity arises from *genetic recombination*, the combining of DNA from two sources. In eukaryotes, the sexual processes of meiosis and fertilization combine DNA from two individuals in a single zygote. But 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*. Although 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 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 Concept 13.1). 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 the process to be 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 (from "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 24.15)**. 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.



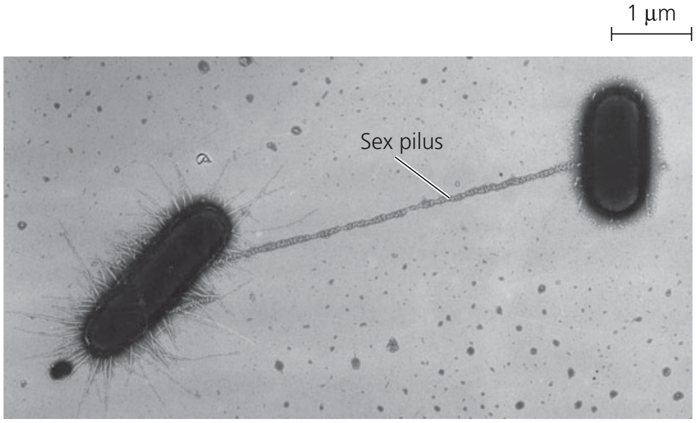
▲ **Figure 24.15 Transduction.** Phages may carry pieces of a bacterial chromosome from one cell (the donor) to another (the recipient). If crossing over occurs after the transfer, genes from the donor may be incorporated into the recipient's genome.

? *Under what circumstances would a transduction event 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. The best-understood mechanism is that used by *E. coli*, and we'll focus on this organism for the rest of this section.

In *E. coli*, a pilus of the donor cell attaches to the recipient **(Figure 24.16)**. The pilus then retracts, pulling the two cells together, much like a grappling hook. The next step is thought to be the formation of a temporary "mating bridge" between the two cells, through which the donor may transfer DNA to the recipient. However, the mechanism by which this transfer oc-



▲ **Figure 24.16 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).

curs is an unsettled issue; indeed, recent evidence suggests that DNA may pass directly through the pilus, which is hollow.

The F Factor However the transfer of DNA takes place, 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. The F factor can exist either as a plasmid or as a segment of DNA within the bacterial chromosome.

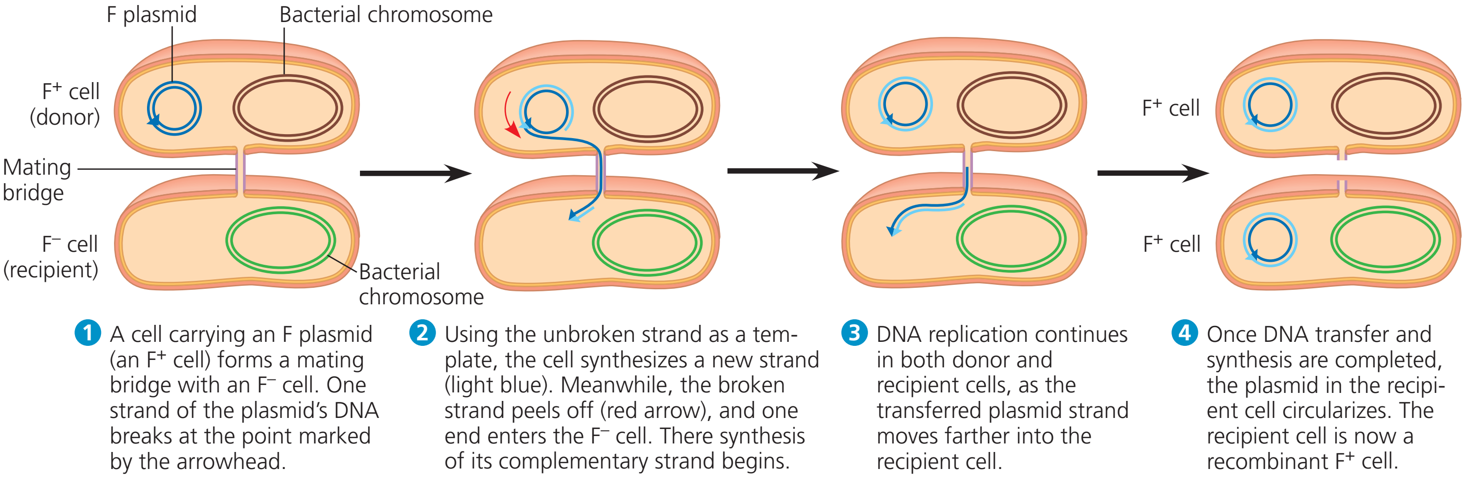
The F factor in its plasmid form is called the **F plasmid**. Cells containing the F plasmid, designated F^+ cells, function as DNA donors during conjugation. Cells lacking the F factor, designated F^-, function as DNA recipients during conjugation. The F^+ condition is transferable in the sense that an F^+ cell converts an F^- cell to F^+ if a copy of the entire F plasmid is transferred **(Figure 24.17)**. In any case, as long as some of the F plasmid's DNA is transferred successfully to the recipient cell, that cell is now a recombinant cell.

A donor cell's F factor can also be integrated into the chromosome. In this case, chromosomal genes can be transferred to a recipient cell during conjugation. When this occurs, homologous regions of the donor and recipient 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 circular chromosomes of two different cells—a new genetic variant on which evolution can act.

R Plasmids and Antibiotic Resistance During the 1950s in Japan, physicians started noticing that some hospital patients with bacterial dysentery, which produces severe diarrhea, did not respond to antibiotics that had been effective in the past. Apparently, resistance to these antibiotics had evolved in some strains of *Shigella*, the bacterium that causes the disease.

Eventually, researchers began to identify the specific genes that confer antibiotic resistance in *Shigella* and other pathogenic bacteria. Sometimes, mutation in a chromosomal gene of the pathogen can confer resistance. For example, a mutation in one gene may make it less likely that the pathogen will transport a particular antibiotic into its cell. Mutation in a different gene may alter the intracellular target protein for an antibiotic molecule, reducing its inhibitory effect. In other cases, bacteria have "resistance genes," which 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).

Exposing a bacterial population to a specific antibiotic will kill antibiotic-sensitive bacteria but not those that happen to have R plasmids with genes that counter the antibiotic. Under these circumstances, we would predict that natural selection would cause the fraction of the bacterial population carrying



▲ **Figure 24.17 Conjugation and transfer of an F plasmid, resulting in recombination.** The DNA replication that accompanies the transfer of an F plasmid is called *rolling circle replication.* In effect, the intact circular DNA strand from the donor cell's F plasmid "rolls" as its other strand peels off and a new complementary strand is synthesized.

genes for antibiotic resistance to increase, and that is exactly what happens. The medical consequences are also predictable: Resistant strains of pathogens are becoming more common, making the treatment of certain bacterial infections more difficult. The problem is compounded by the fact that many R plasmids, like F plasmids, have genes that encode pili and enable DNA transfer from one bacterial cell to another by conjugation. Making the problem still worse, some R plasmids carry as many as ten genes for resistance to that many antibiotics.

CONCEPT CHECK 24.3

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 of transferring DNA from one bacterial cell to another.
3. In a rapidly changing environment, which bacterial population would likely be more successful, one that includes individuals capable of conjugation or one that does not? Explain.
4. **WHAT IF?** If a nonpathogenic bacterium were to acquire resistance to antibiotics, could this strain pose a health risk to people? Explain. In general, how does DNA transfer among bacteria affect the spread of resistance genes?

For suggested answers, see Appendix A.

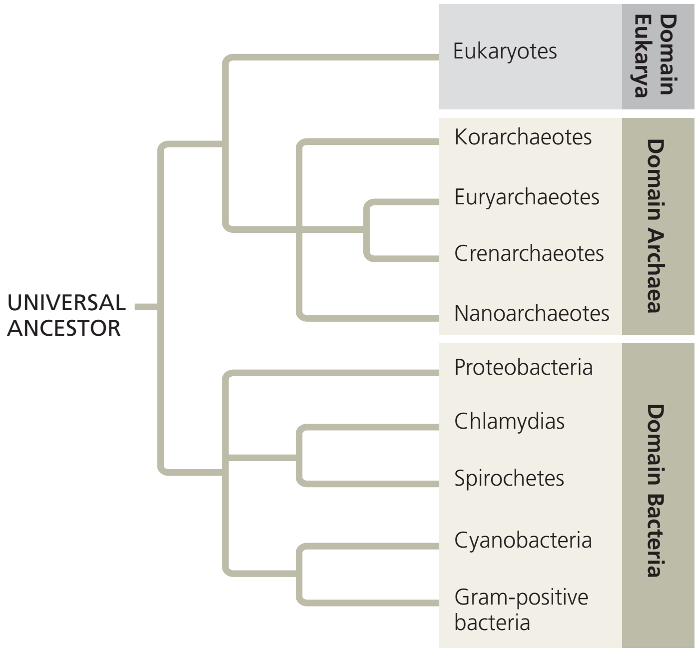
CONCEPT 24.4

Prokaryotes have radiated into a diverse set of lineages

Since their origin 3.5 billion years ago, prokaryotic populations have radiated extensively as they acquired diverse structural and metabolic adaptations. 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 we have begun to uncover the full extent of prokaryotic diversity.

An Overview of Prokaryotic Diversity

Microbiologists began comparing the sequences of prokaryotic genes in the 1970s. For example, using small-subunit ribosomal RNA as a marker for evolutionary relationships, researchers concluded 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 taxonomic groups, such as cyanobacteria, are monophyletic. However, other traditional groups, such as gram-negative bacteria, are scattered throughout several lineages. **Figure 24.18** shows one phylogenetic hypothesis for some of the major taxa of prokaryotes based on molecular systematics.



▲ **Figure 24.18 A simplified phylogeny of prokaryotes.** This phylogenetic tree based on molecular data shows one of several debated hypotheses of the relationships between the major prokaryotic groups discussed in this chapter. Within Archaea, the placement of the korarchaeotes and nanoarchaeotes remains unclear.

? *Which domain is the sister group of Archaea?*

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 13.25) 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 18.1). Each year, these techniques add new branches to the tree of life. While only about 9,800 prokaryotic species 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.

Another important lesson from molecular systematics is that horizontal gene transfer has played a major 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 2011 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 discussed in Chapter 20, 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 24.18).

Bacteria

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. Every major mode of nutrition and metabolism is represented among bacteria, and even a small taxonomic 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. **Figure 24.19**, on the next two pages, provides a closer look at several major groups of bacteria.

Archaea

Archaea share certain traits with bacteria and other traits with eukaryotes **(Table 24.2)**. 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 and the Dead Sea. 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 walls of archaea in the genus *Halobacterium* have unusual features that improve function in extremely salty environments but render these organisms incapable of survival if the salinity drops below 9%.

Extreme thermophiles (from the Greek *thermos*, hot) thrive in very hot environments **(Figure 24.20)**. For example, archaea in the genus *Sulfolobus* live in sulfur-rich volcanic springs as hot as 90°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. *Sulfolobus* and other extreme thermophiles avoid this fate because they have structural and biochemical adaptations that make their DNA and proteins stable at high temperatures. 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. Another extreme thermophile, *Pyrococcus furiosus*, is used in biotechnology as a source of DNA polymerase for the PCR technique.

Many other archaea live in more moderate environments. Consider the **methanogens**, archaea that release methane as

Table 24.2 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

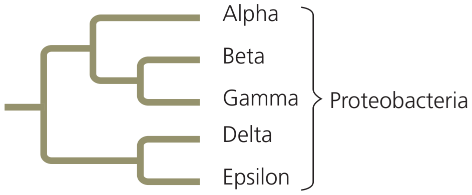
▲ **Figure 24.20 Extreme thermophiles.** Orange and yellow colonies of thermophilic prokaryotes grow in the hot water of Yellowstone National Park's Grand Prismatic Spring.

MAKE CONNECTIONS *Review the discussion of enzymes in Concept 6.4. How might the enzymes of thermophiles differ from those of other organisms?*

▼ Figure 24.19 Exploring Major Groups of Bacteria

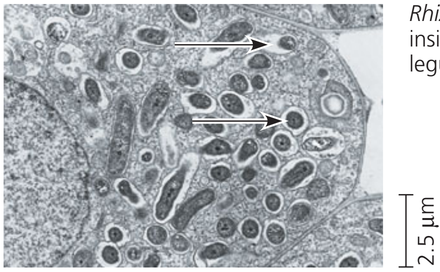
Proteobacteria

This large and diverse clade of gram-negative bacteria includes photoautotrophs, chemoautotrophs, and heterotrophs. Some proteobacteria are anaerobic, while others are aerobic. Molecular systematists currently recognize five subgroups of proteobacteria; the phylogenetic tree at right shows their relationships based on molecular data.



Subgroup: Alpha Proteobacteria

Many of the species in this subgroup are closely associated with eukaryotic hosts. For example, *Rhizobium* species live in nodules within the roots of legumes (plants of the pea/bean family), where the bacteria convert atmospheric N_2 to compounds the host plant can use to make proteins. Species in the genus *Agrobacterium* produce tumors in plants; genetic engineers use these bacteria to carry foreign DNA into the genomes of crop plants. Scientists hypothesize that mitochondria evolved from aerobic alpha proteobacteria through endosymbiosis.



Rhizobium (arrows) inside a root cell of a legume (TEM)

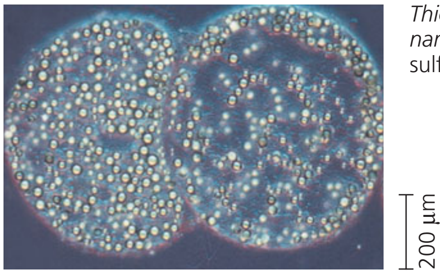
Subgroup: Beta Proteobacteria

This nutritionally diverse subgroup includes *Nitrosomonas*, a genus of soil bacteria that play an important role in nitrogen recycling by oxidizing ammonium (NH_4^+), producing nitrite (NO_2^-) as a waste product.

Nitrosomonas (colorized TEM)

Subgroup: Gamma Proteobacteria

This subgroup's autotrophic members include sulfur bacteria, such as *Thiomargarita namibiensis*, which obtain energy by oxidizing H_2S, producing sulfur as a waste product (the small globules in the photograph at right). Some heterotrophic gamma proteobacteria are pathogens; for example, *Legionella* causes Legionnaires' disease, *Salmonella* is responsible for some cases of food poisoning, and *Vibrio cholerae* causes cholera. *Escherichia coli,* a common resident of the intestines of humans and other mammals, normally is not pathogenic.



Thiomargarita namibiensis containing sulfur wastes (LM)

Subgroup: Delta Proteobacteria

This subgroup includes the slime-secreting myxobacteria. When the soil dries out or food is scarce, the cells congregate into a fruiting body that releases resistant "myxospores." These cells found new colonies in favorable environments. Another group of delta proteobacteria, the bdellovibrios, attack other bacteria, charging at up to 100 µm/sec (comparable to a human running 240 km/hr). The attack begins when a bdellovibrio attaches to specific molecules found on the outer covering of some bacterial species. The bdellovibrio then drills into its prey by using digestive enzymes and spinning at 100 revolutions per second.

Fruiting bodies of *Chondromyces crocatus,* a myxobacterium (SEM)

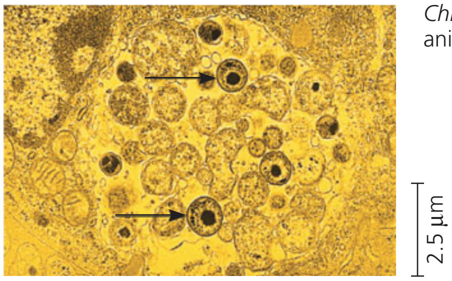
Subgroup: Epsilon Proteobacteria

Most species in this subgroup are pathogenic to humans or other animals. Epsilon proteobacteria include *Campylobacter*, which causes blood poisoning and intestinal inflammation, and *Helicobacter pylori*, which causes stomach ulcers.

Helicobacter pylori (colorized TEM)

Chlamydias

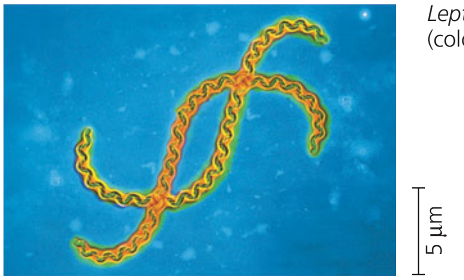
These parasites can survive only within animal cells, depending on their hosts for resources as basic as ATP. The gram-negative walls of chlamydias are unusual in that they lack peptidoglycan. One species, *Chlamydia trachomatis,* is the most common cause of blindness in the world and also causes nongonococcal urethritis, the most common sexually transmitted disease in the United States.



Chlamydia (arrows) inside an animal cell (colorized TEM)

Spirochetes

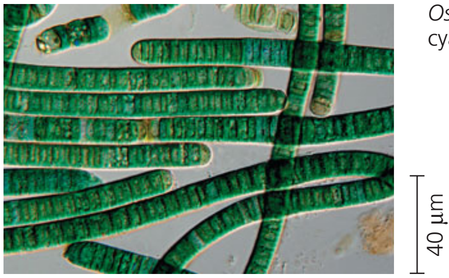
These helical gram-negative heterotrophs spiral through their environment by means of rotating, internal, flagellum-like filaments. Many spirochetes are free-living, but others are notorious pathogenic parasites: *Treponema pallidum* causes syphilis, and *Borrelia burgdorferi* causes Lyme disease.



Leptospira, a spirochete (colorized TEM)

Cyanobacteria

These gram-negative photoautotrophs are the only prokaryotes with plantlike, oxygen-generating photosynthesis. (In fact, chloroplasts likely evolved from an endosymbiotic cyanobacterium.) Both solitary and filamentous cyanobacteria are abundant components of freshwater and marine *phytoplankton*, the collection of photosynthetic organisms that drift near the water's surface. Some filaments have cells specialized for nitrogen fixation, the process that incorporates atmospheric N_2 into inorganic compounds that can be used in the synthesis of amino acids and other organic molecules.



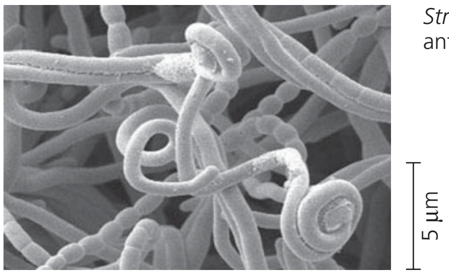
Oscillatoria, a filamentous cyanobacterium

Gram-Positive Bacteria

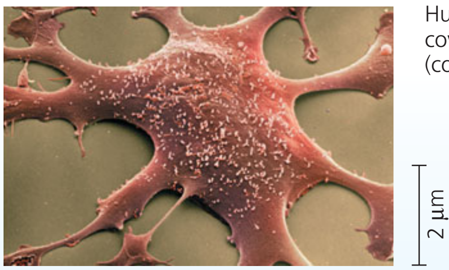
Gram-positive bacteria rival the proteobacteria in diversity. Species in one subgroup, the actinomycetes (from the Greek *mykes,* fungus, for which these bacteria were once mistaken), form colonies containing branched chains of cells. Two species of actinomycetes cause tuberculosis and leprosy. However, most actinomycetes are free-living species that help decompose the organic matter in soil; their secretions are partly responsible for the "earthy" odor of rich soil. Soil-dwelling species in the genus *Streptomyces* (top) are cultured by pharmaceutical companies as a source of many antibiotics, including streptomycin.

Gram-positive bacteria include many solitary species, such as *Bacillus anthracis*, which causes anthrax, and *Clostridium botulinum*, which causes botulism. The various species of *Staphylococcus* and *Streptococcus* are also gram-positive bacteria.

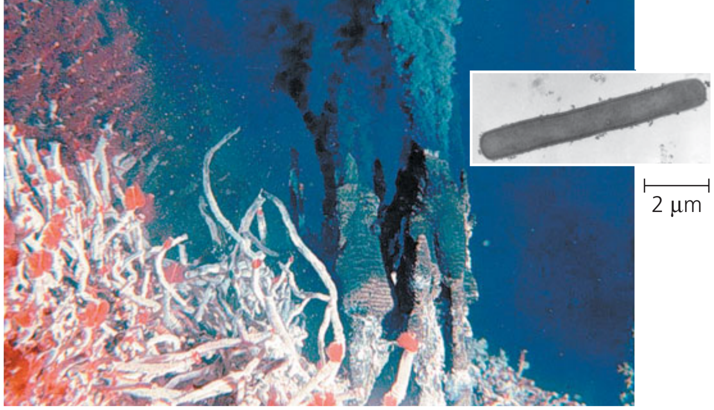
Mycoplasmas (bottom) are the only bacteria known to lack cell walls. They are also the tiniest known cells, with diameters as small as 0.1 μm, only about five times as large as a ribosome. Mycoplasmas have small genomes—*Mycoplasma genitalium* has only 517 genes, for example. Many mycoplasmas are free-living soil bacteria, but others are pathogens.



Streptomyces, the source of many antibiotics (SEM)



Hundreds of mycoplasmas covering a human fibroblast cell (colorized SEM)



▲ **Figure 24.21 A highly thermophilic methanogen.** The archaean *Methanopyrus kandleri* (inset) lives in the extreme heat of "black smoker" hydrothermal vents on the ocean floor.

a by-product of their unique ways of obtaining 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 around deep-sea hydrothermal vents **(Figure 24.21)**, others live in swamps 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 of methanogens inhabit the anaerobic environment within the guts of cattle, termites, and other herbivores, playing an essential role in the nutrition of these animals. Methanogens also have an important application as decomposers in sewage treatment facilities.

Many extreme halophiles and all known methanogens are archaea in the clade Euryarchaeota (from the Greek *eurys*, broad, a reference to the habitat range of these prokaryotes). 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). Recent 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 waters of the open ocean.

New findings continue to update the picture of archaeal phylogeny. In 1996, researchers sampling a hot spring in Yellowstone National Park discovered archaea that do not appear to belong to either Euryarchaeota or Crenarchaeota. They placed these archaea in a new clade, Korarchaeota (from the Greek *koron*, young man). In 2002, researchers exploring hydrothermal vents off the coast of Iceland discovered archaeal cells only 0.4 µm in diameter attached to a much larger crenarchaeote. The genome of the smaller archaean is one of the smallest known of any organism, containing only 500,000 base pairs. Genetic analysis indicates that this prokaryote belongs to a fourth archaeal clade, Nanoarchaeota (from the Greek *nanos*, dwarf). Within a year after this clade was named, three other DNA sequences from nanoarchaeote species were isolated: one from Yellowstone's hot springs, one from hot springs in Siberia, and one from a hydrothermal vent in the Pacific. As metagenomic prospecting continues, the tree in Figure 24.18 may well undergo further changes.

CONCEPT CHECK 24.4

1. Explain how molecular systematics has contributed to our understanding of the phylogeny and evolution of prokaryotes.
2. How has metagenomics contributed to our understanding of prokaryotic diversity and phylogeny?
3. **WHAT IF?** What would the discovery of a bacterial species that is a methanogen imply about the evolution of the methane-producing pathway?

For suggested answers, see Appendix A.

CONCEPT 24.5

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.

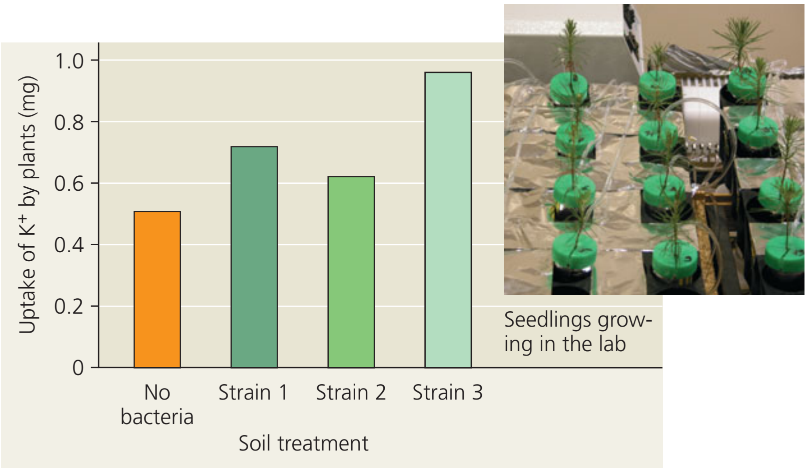
Chemical Recycling

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 there. 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, 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 Chapter 42 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 24.22)**. Prokaryotes can also *decrease* the availability of key plant nutrients; this occurs when prokaryotes "immobilize" nutrients by using them to synthesize molecules that remain within their cells. Thus, prokaryotes can have complex effects on soil nutrient

▶ **Figure 24.22 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.

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?*



concentrations. In marine environments, a recent study found that an archaean from the clade Crenarchaeota can perform nitrification, a key step in the nitrogen cycle (see Figure 42.13). Crenarchaeotes dominate the oceans by numbers, comprising an estimated 10^{28} cells. Their abundance suggests that these organisms may have a large impact on the global nitrogen cycle; scientists are investigating this possibility.

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 24.23)**. Other interactions take the form of **commensalism**, an interaction 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 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 prokaryotes engage in **parasitism**, an interaction in which a **parasite** eats 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. (Chapter 41 discusses mutualism, commensalism, and parasitism in more detail.)

▲ **Figure 24.23 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.

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.

Impact on Humans

Though 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

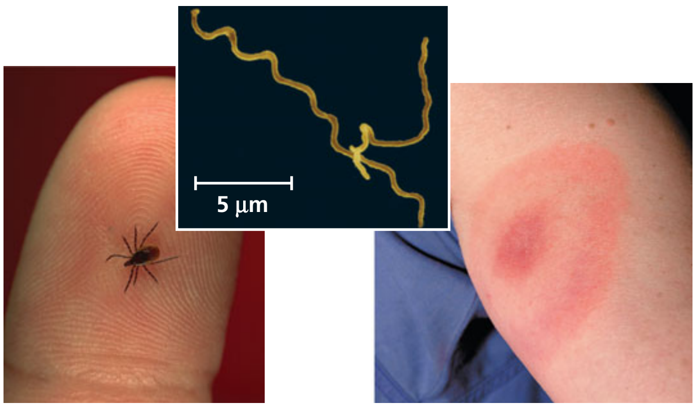
As is true for many other eukaryotes, human well-being can depend on mutualistic prokaryotes. For example, our intestines are home to an estimated 500–1,000 species of bacteria; their cells outnumber all human cells in the body by a factor of ten. Different species live in different portions of the intestines, 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. In 2003, scientists published the first complete genome of one of these gut mutualists, *Bacteroides thetaiotaomicron*. The genome includes a large array of genes involved in synthesizing carbohydrates, vitamins, and other nutrients needed by 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, about 2 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 15,000 to 20,000 people each year **(Figure 24.24)**. Caused by a bacterium carried by ticks that live on deer and field mice, 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



▲ **Figure 24.24 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.

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 not present. In one such case, eight people contracted botulism after eating salted fish that did not contain any *C. botulinum* bacteria, but did contain the botulinum toxin. Even though the bacterium was no longer present, at some point in the fish preparation process the bacterium must have been able to grow and secrete the toxin.

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.

Since the 19th century, improved sanitation systems in the industrialized world have greatly reduced the threat of pathogenic bacteria. Antibiotics have saved a great many lives and reduced the incidence of disease. However, resistance to antibiotics is currently evolving in many bacterial strains. As you read earlier, the rapid reproduction of bacteria enables cells carrying resistance genes to quickly give rise to large populations as a result of natural selection, and these genes can also spread to other species by horizontal gene transfer.

Horizontal gene transfer can also 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 75,000 cases of O157:H7 infection per year, often from contaminated beef or produce. In 2001, scientists sequenced the genome of O157:H7 and compared it with the genome of a harmless strain of *E. coli* called K-12. They discovered that 1,387 out of the 5,416 genes in O157:H7 have no counterpart in K-12. Many of these 1,387 genes are found in chromosomal regions that include phage DNA. This suggests that at least some of the 1,387 genes were incorporated into the genome of O157:H7 through phage-mediated horizontal gene transfer (transduction). Some of the genes found only in O157:H7 are associated with virulence, including genes that code for adhesive fimbriae that enable O157:H7 to attach itself to the intestinal wall and extract nutrients.

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. In recent years, our greater understanding of prokaryotes has led

Scientific Skills Exercise

Making a Bar Graph and Interpreting Data

Do Soil Microorganisms Protect Against Crop Disease? The soil layer surrounding plant roots, called the *rhizosphere*, is a complex community in which archaea, bacteria, fungi, and plants interact with one another. When crop plants are attacked by fungal or bacterial pathogens, in some cases soil from the rhizosphere protects plants from future attacks. Such protective soil is called disease-suppressive soil. Plants grown in disease-suppressive soils appear to be less vulnerable to pathogen attack. In this exercise, you'll interpret data from an experiment studying whether microorganisms were responsible for the protective effects of disease-suppressive soils.

How the Experiment Was Done The researchers obtained disease-suppressive soil from 25 random sites in an agricultural field in the Netherlands in which sugar beet crops had previously been attacked by *Rhizoctonia solani*, a fungal pathogen that also afflicts potatoes and rice. The researchers collected other soil samples from the grassy margins of the field where sugar beets had not been grown. The researchers predicted that these soil samples from the margins would not offer protection against pathogens.

The researchers then planted and raised sugar beets in greenhouses, using 5 different soil treatments. Each soil treatment was applied to 4 pots, and each pot contained 8 plants. The pots were inoculated with *Rhizoctonia solani*. After 20 days, researchers determined the percentage of infected sugar beet seedlings for each soil treatment.

Data from the Experiment

Soil Treatment	Percentage of Seedlings with Fungal Disease
Disease-suppressive soil	3.0
Soil from margin of field	62
Soil from margin of field + 10% disease-suppressive soil	39
Disease-suppressive soil heated to 50°C for 1 hour	31
Disease-suppressive soil heated to 80°C for 1 hour	70

Interpret the Data

1. What hypothesis were the researchers testing in this study? What is the independent variable in this study? What is the dependent variable?
2. What is the total number of pots used in this experiment, and how many plants received each soil treatment? Explain why multiple pots and plants were used for each treatment.
3. Use the data in the table to create a bar graph. Then in words, describe and compare the results for the five soil treatments.
4. The researchers stated, "Collectively, these results indicated that disease suppressiveness [of soil] toward *Rhizoctonia solani* was microbiological in nature." Is this statement supported by the results shown in the graph? Explain.

Data from R. Mendes, et al. Deciphering the rhizosphere for disease-suppressive bacteria, *Science* 332: 1097–1100 (2011).

MB A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

to an explosion of new applications in biotechnology; two examples are the use of *E. coli* in gene cloning (see Figure 13.22) and the use of *Agrobacterium tumefaciens* in producing transgenic plants. Naturally occurring soil bacteria may have potential for combating diseases that affect crop plants; in the **Scientific Skills Exercise**, you can interpret data from an experiment studying the effect of these bacteria.

Bacteria may soon figure prominently in another major industry: plastics. Globally, each year about 350 billion pounds of plastic are produced from petroleum and used to make toys, storage containers, soft drink bottles, and many other items. These products degrade slowly, creating environmental problems. Bacteria can now be used to make natural plastics **(Figure 24.25a)**. For example, some bacteria synthesize a type of polymer known as PHA (polyhydroxyalkanoate), which they use to store chemical energy. The PHA they produce can be extracted, formed into pellets, and used to make durable, yet biodegradable plastics. Through genetic engineering, we can now modify bacteria to produce vitamins, antibiotics, hormones, and other products (see Concept 13.4). Researchers are seeking to reduce fossil fuel use by engineering bacteria that can produce ethanol from various forms of biomass, including agricultural waste, switchgrass, municipal waste (such as paper products that are not recycled), and corn (**Figure 24.25b**).

Another way to harness prokaryotes is in **bioremediation**, the use of organisms to remove pollutants from soil, air, or 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

▲ **Figure 24.25 Products from prokaryotes. (a)** These bacteria synthesize and store PHA, which can be extracted and used to make biodegradable plastic products. **(b)** Current research seeks to develop bacteria that produce ethanol (E-85) fuel efficiently from renewable plant products.

▲ **Figure 24.26 Bioremediation of an oil spill.** Spraying fertilizers on an oil-soaked area stimulates growth of native bacteria that metabolize the oil. This can speed up the natural breakdown process by a factor of five.

spills (**Figure 24.26**) 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, to which we devote the remainder of this unit.

CONCEPT CHECK 24.5

1. Explain how prokaryotes, though small, can be considered giants in their collective impact on Earth and its life.
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. **MAKE CONNECTIONS** Review photosynthesis in Figure 8.5. Then summarize the main steps by which cyanobacteria produce O_2 and use CO_2 to make organic compounds.
4. **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.

24 Chapter Review

SUMMARY OF KEY CONCEPTS

CONCEPT 24.1

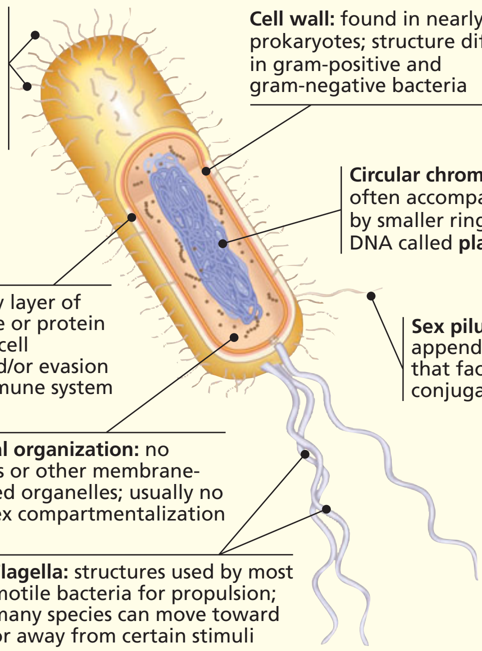
Conditions on early Earth made the origin of life possible (pp. 459–462)

- 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-enclosed droplets that have some properties of cells.
- The first genetic material may have been short pieces of RNA capable of guiding polypeptide synthesis and self-replication. Early protocells containing such RNA would have increased through natural selection.
- Fossil evidence of early prokaryotes dates to 3.5 billion years ago. By 2.8 billion years ago, prokaryotes included stromatolites that differed in morphology and habitat. Early prokaryotes also included cyanobacteria that released oxygen as a by-product of photosynthesis, thereby changing Earth's atmosphere and altering the course of evolution.

? *Describe the roles that montmorillonite clay and vesicles may have played in the origin of life.*

CONCEPT 24.2

Diverse structural and metabolic adaptations have evolved in prokaryotes (pp. 462–467)



- Nutritional diversity is much greater in prokaryotes than in eukaryotes. As a group, prokaryotes perform 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. In *Anabaena*, photosynthetic cells and nitrogen-fixing cells exchange metabolic products. Metabolic cooperation also occurs in surface-coating **biofilms** that include different species.
- Prokaryotes can reproduce quickly by binary fission.

? *Describe features of prokaryotes that enable them to thrive in a wide range of different environments.*

CONCEPT 24.3

Rapid reproduction, mutation, and genetic recombination promote genetic diversity in prokaryotes (pp. 467–470)

- 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, genetic recombination can promote adaptive evolution in prokaryotic populations.

? *Although prokaryotes reproduce asexually, their populations can have high genetic diversity. Explain how this can occur.*

CONCEPT 24.4

Prokaryotes have radiated into a diverse set of lineages (pp. 470–474)

- Molecular systematics is leading to a phylogenetic classification of prokaryotes, allowing systematists to identify major new clades.
- Some archaea, such as **extreme thermophiles** and **extreme halophiles**, live in extreme environments. Other archaea live in moderate environments, such as soils and lakes.
- Diverse nutritional types are scattered among the major groups of bacteria. The two largest groups are the proteobacteria and gram-positive bacteria.

? *What impact have molecular data had on constructing prokaryotic phylogeny?*

CONCEPT 24.5

Prokaryotes play crucial roles in the biosphere (pp. 474–478)

- 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.
- 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 previously harmless species or strains.
- Experiments with bacteria such as *E. coli* have led to important advances in DNA technology. Prokaryotes can be used in bioremediation and in the synthesis of vitamins, antibiotics, and other products.

? *In what ways are prokaryotes key to the survival of many species?*

TEST YOUR UNDERSTANDING

Level 1: Knowledge/Comprehension

1. Which of the following steps has *not* yet been accomplished by scientists studying the origin of life?
   a. synthesis of small RNA polymers by ribozymes
   b. abiotic synthesis of polypeptides
   c. formation of molecular aggregates with selectively permeable membranes
   d. formation of protocells that use DNA to direct the polymerization of amino acids
   e. abiotic synthesis of organic molecules

2. Fossilized stromatolites
   a. more than 2.8 billion years old have not been discovered.
   b. formed around deep-sea vents.
   c. resemble structures formed by bacterial communities that are found today in some shallow marine bays.
   d. provide evidence that plants moved onto land in the company of fungi around 500 million years ago.
   e. contain the first undisputed fossils of eukaryotes and date from 1.8 billion years ago.

3. Genetic variation in bacterial populations cannot result from
   a. transduction.
   b. transformation.
   c. conjugation.
   d. mutation.
   e. meiosis.

4. Photoautotrophs use
   a. light as an energy source and methane as a carbon source.
   b. light as an energy source and CO_2 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.
   e. H_2S as an energy source and CO_2 as a carbon source.

5. Which of the following statements is *not* true?
   a. Archaea and bacteria have different membrane lipids.
   b. Both archaea and bacteria generally lack membrane-enclosed organelles.
   c. The cell walls of archaea lack peptidoglycan.
   d. Only bacteria have histones associated with DNA.
   e. Only some archaea use CO_2 to oxidize H_2, releasing methane.

6. Bacteria perform the following ecological roles. Which role typically does *not* involve symbiosis?
   a. skin commensalist
   b. pathogen
   c. bioluminescent bacteria in fish
   d. gut mutualist
   e. decomposer

7. Plantlike photosynthesis that releases O_2 occurs in
   a. cyanobacteria.
   b. chlamydias.
   c. archaea.
   d. actinomycetes.
   e. chemoautotrophic bacteria.

Level 2: Application/Analysis

8. **SCIENTIFIC INQUIRY**
   DRAW IT 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 your graph.

Rhizobium strain	1	2	3	4	5	6
Plant mass (g)	0.91	0.06	1.56	1.72	0.14	1.03

Source 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.

Level 3: Synthesis/Evaluation

9. **FOCUS ON EVOLUTION**
   In patients infected 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. How might this result in the evolution of drug-resistant pathogens?

10. **FOCUS ON ENERGY AND MATTER**
    In a short essay (about 100–150 words), discuss how prokaryotes and other members of hydrothermal vent communities transfer and transform energy.

For selected answers, see Appendix A.

25 The Origin and Diversification of Eukaryotes

KEY CONCEPTS

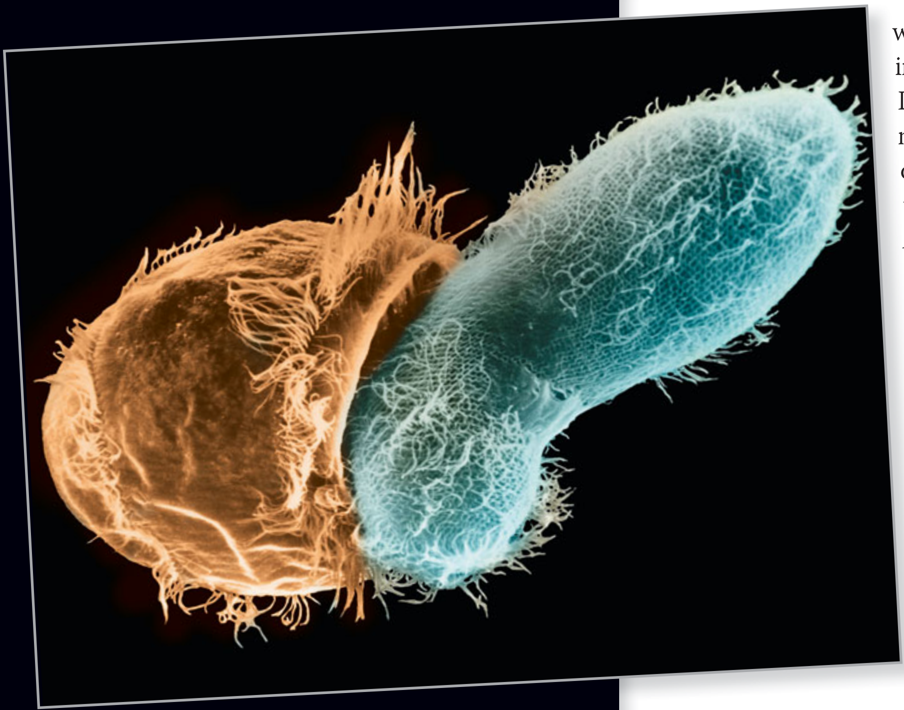
25.1 Eukaryotes arose by endosymbiosis more than 1.8 billion years ago

25.2 Multicellularity has originated several times in eukaryotes

25.3 Four "supergroups" of eukaryotes have been proposed based on morphological and molecular data

25.4 Single-celled eukaryotes play key roles in ecological communities and affect human health

▼ **Figure 25.1** What enables the cell on the left to engulf its prey?



OVERVIEW

Shape Changers

The organisms in **Figure 25.1** are ciliates, a diverse group of single-celled eukaryotes named after the small appendages—cilia—that cover much of their bodies and enable them to move. The ciliate on the left, *Didinium*, has begun a seemingly impossible task: it will completely engulf the *Paramecium* (right), even though the *Paramecium* is as large as it is.

Reflect for a moment on the magnitude of this feat. If we humans could do this, in a single swallow we could ingest more food than we would typically eat in a month. Like us, even the prokaryotes discussed in Chapter 24 cannot engulf food items their own size—although prokaryotes can metabolize an astonishing range of compounds, they can only absorb small particles of food. What enables *Didinium* to tackle food items that could easily evade a hungry prokaryote?

One key to *Didinium*'s success lies within its cells—it has a complex set of cytoskeletal proteins that enable the cell to change in shape dramatically as it feeds. *Didinium* also has small structures similar to miniature harpoons that it can eject to help ensnare its prey. These two features illustrate the structural complexity that characterizes the cells of *Didinium* and the other diverse, mostly unicellular groups of eukaryotes informally known as **protists**.

As we'll see, some protists change their form as they creep along using blob-like appendages, others are shaped like tiny trumpets, and still others resemble miniature jewelry. In this chapter, we'll explore how these shape-changing, structurally complex eukaryotic cells arose from their morphologically simpler prokaryotic ancestors. We'll also examine another major step in the evolutionary history of life: the origin of multicellular eukaryotes such as plants, fungi, and animals. Finally, we'll consider how single-celled eukaryotes affect ecosystems and human health.

CONCEPT 25.1

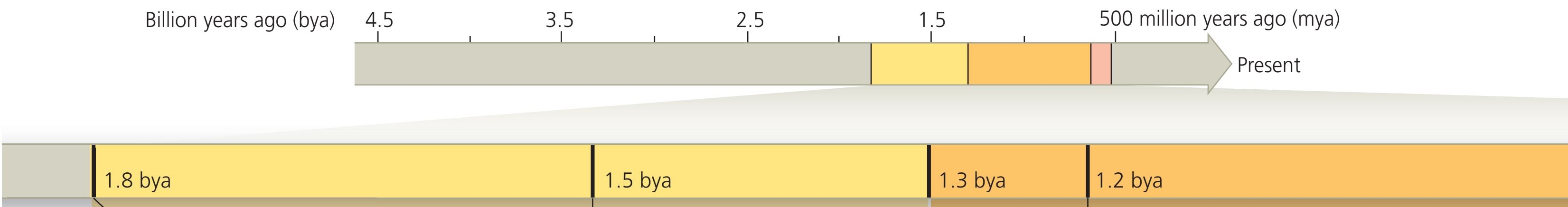
Eukaryotes arose by endosymbiosis more than 1.8 billion years ago

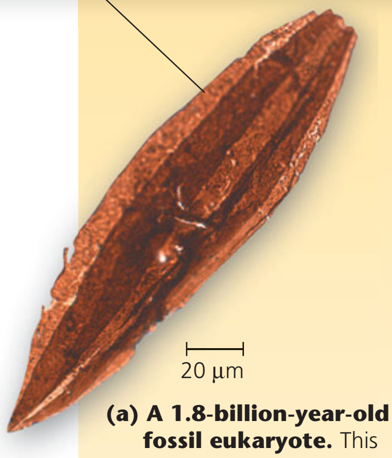
As we discussed in Chapter 24, all organisms were unicellular early in the history of life. The evolution of eukaryotes did not immediately change this, but it did involve fundamental changes in the structure of these individual cells. For example, unlike the cells of prokaryotes, the cells of all eukaryotes 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 that of prokaryotic cells.

Another key eukaryote characteristic is a well-developed cytoskeleton that extends throughout the cell (see Figure 4.20). The cytoskeleton provides structural support that enables eukaryotic cells to have asymmetric (irregular) forms, as well as to change shape as they feed, move, or grow. Although some prokaryotes have proteins related to eukaryotic cytoskeletal proteins, their rigid cell walls and lack of a well-developed cytoskeleton limit the extent to which their cells can maintain asymmetric forms or change shape over time.

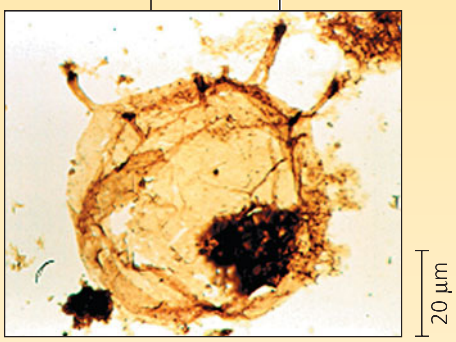
The fossil record indicates that prokaryotes were inhabiting Earth at least 3.5 billion years ago (see Chapter 24). At what

▼ Figure 25.2 Exploring the Early Evolution of Eukaryotes





(a) A 1.8-billion-year-old fossil eukaryote. This ancient organism had a cell wall structure similar to that of some living algae, but different from that of prokaryotes—indicating this fossil organism was an early eukaryote.



(b) *Tappania*, a 1.5-billion-year-old fossil that may represent an early alga or fungus. Many fossils of this organism have been found; the number, size, and location of the structures protruding from the cell's outer surface vary from one individual to another.

(c) *Bangiomorpha*, an ancient red alga. Fossils show that this species had three distinct cell types, direct evidence of complex multicellularity. All of the cells shown here are non-reproductive (vegetative) cells; some of these cells will produce spores later in development.

Initial Diversification

The fossil record shows that a moderate diversity of single-celled eukaryotes was already present 1.8 billion years ago, including the fossil specimen in **(a)**. Researchers have discovered other fossil eukaryotes of the same age that vary in size and had shapes ranging from spherical to elliptical (some that are spindle-shaped, or tapering at each end). This variety suggests that the eukaryotes may have originated much earlier in time.

Early members of domain Eukarya had a nucleus, a flexible membrane, and a cytoskeleton capable of supporting an irregular cell shape, like that seen in **(b)**. Other fossils from this time period include several different types of simple filaments thought to be of small, multicellular eukaryotes. Although fossil eukaryotes from this time range are moderately diverse, none of these organisms can be assigned with confidence to an extant group of eukaryotes.

(*Time line not to scale.*)

Appearance of Novel Features

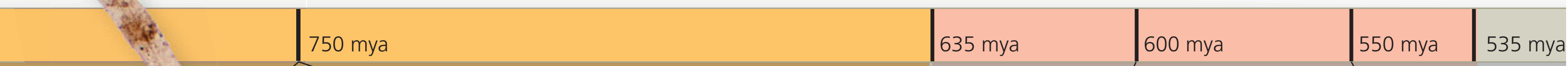
The oldest known eukaryotic fossils that can be resolved taxonomically are of small red algae that lived 1.2 billion years ago **(c)**; note that **algae** is a general term that includes all groups of photosynthetic protists. Other fossils from this period include green algae **(d)** and certain types of amoebas that lived within vase-shaped structures **(e)**, as well as a variety of colonial and multicellular protists of unknown taxonomic affinity.

The taxonomic diversification seen in these fossils was accompanied by a suite of novel biological features, including the origins of complex multicellularity (a term that applies to multicellular organisms with differentiated cell types), sexual life cycles, and eukaryotic photosynthesis. Some of these features can be point did irregular forms and other novel features of eukaryotes appear, signifying the origin of the group? Fossils and molecular data provide clues to when and how eukaryotes may have arisen from their prokaryotic ancestors.

The Fossil Record of Early Eukaryotes

Complex lipids that are synthesized by eukaryotes (but not by prokaryotes) have been found in rocks dated to 2.7 billion years ago. Although such chemical evidence is consistent with eukaryotes having lived at that time, the oldest widely accepted fossils of eukaryotic organisms are 1.8 billion years old. Over time, the descendants of these organisms gave rise to the rich diversity of protists and other eukaryotes alive today.

Figure 25.2 surveys how that diversity arose, focusing on three stages documented by the fossil record: an initial diversification (1.8–1.3 billion years ago), the origin of multicellularity and other novel features (1.3 billion–635 million years ago), and the emergence of large eukaryotes (635–535 million years ago).



(d) *Proterocladus*, classified as a green alga.

(e) *Bonneia*, a vase-shaped eukaryote. Found worldwide in 750 million-year-old rocks, this microfossil species lived in organic-rich marine environments and probably grazed on the microbial mats that were widespread at that time.

(f) An early member of the Ediacaran biota. The alga *Doushantuophyton* lived about 600 million years ago.

(g) *Spriggina floundersi*, an early animal with many body segments.

observed directly, while others are inferred from living members of the group to which a fossil belongs. For example, *Bangiomorpha* (c) had "holdfasts" similar to those that anchor living red algae to their substrate; it also had a pattern of cell division that is only known to occur in a particular group of extant red algae. Hence, *Bangiomorpha* is classified as a member of this group of red algae. Living members of this group have sexual life cycles and are photosynthetic, so it is likely that *Bangiomoprha* also had these features.

A range of other fossils show that by 800–750 million years ago, increasingly complex communities of eukaryotes had emerged, with algae at the bottom of the food chain and species that ate algae (or each other) above. These organisms remained small, however, and the entire community began to decline with the onset of a series of severe ice ages and other environmental changes.

Rise of Large Eukaryotes

For nearly 3 billion years, life on Earth was a world of microscopic forms. Larger multicellular eukaryotes do not appear in the fossil record until the Ediacaran period, 635-542 million years ago **(f, g)**. These fossils, referred to as the **Ediacaran biota**, were of soft-bodied organisms, some over 1 m long.

More generally, the fossil record from 635-535 million years ago documents changes in the history of life: maximum body size, taxonomic diversity, and the extent of morphological differences all increased dramatically. In addition, the average time that species persisted in the fossil record dropped considerably. Indeed, the entire Ediacaran biota declined 535 million years ago with the onset of another great wave of evolutionary diversification—the so-called "Cambrian explosion."

As discussed in Figure 25.2, large, multicellular eukaryotes did not appear until about 600 million years ago. Prior to that time, Earth was a microbial world: Its only inhabitants were single-celled prokaryotes and eukaryotes, along with an assortment of microscopic, multicellular eukaryotes. We'll return to the rise of large, multicellular eukaryotes in Chapters 26 and 27.

Endosymbiosis in Eukaryotic Evolution

The fossil record documents when early eukaryotes lived and when key eukaryotic traits, such as a well-developed cytoskeleton and sexual life cycles, first appeared. Additional insights into the origin of eukaryotes have come from molecular studies. In particular, DNA sequence data suggest that eukaryotes are "combination" organisms, with some of their genes and cellular characteristics being derived from archaea, and others from bacteria **(Table 25.1)**.

How did eukaryotes come to have both archaeal and bacterial features? This mixture of features may be a consequence of **endosymbiosis**, a symbiotic relationship in which one organism lives inside the body or cell of another organism. According to this hypothesis, the defining moment in the origin of eukaryotes occurred when an archaeal cell (or a cell with archaeal ancestors) engulfed a bacterium that would later become an organelle found in all eukaryotes—the mitochondrion.

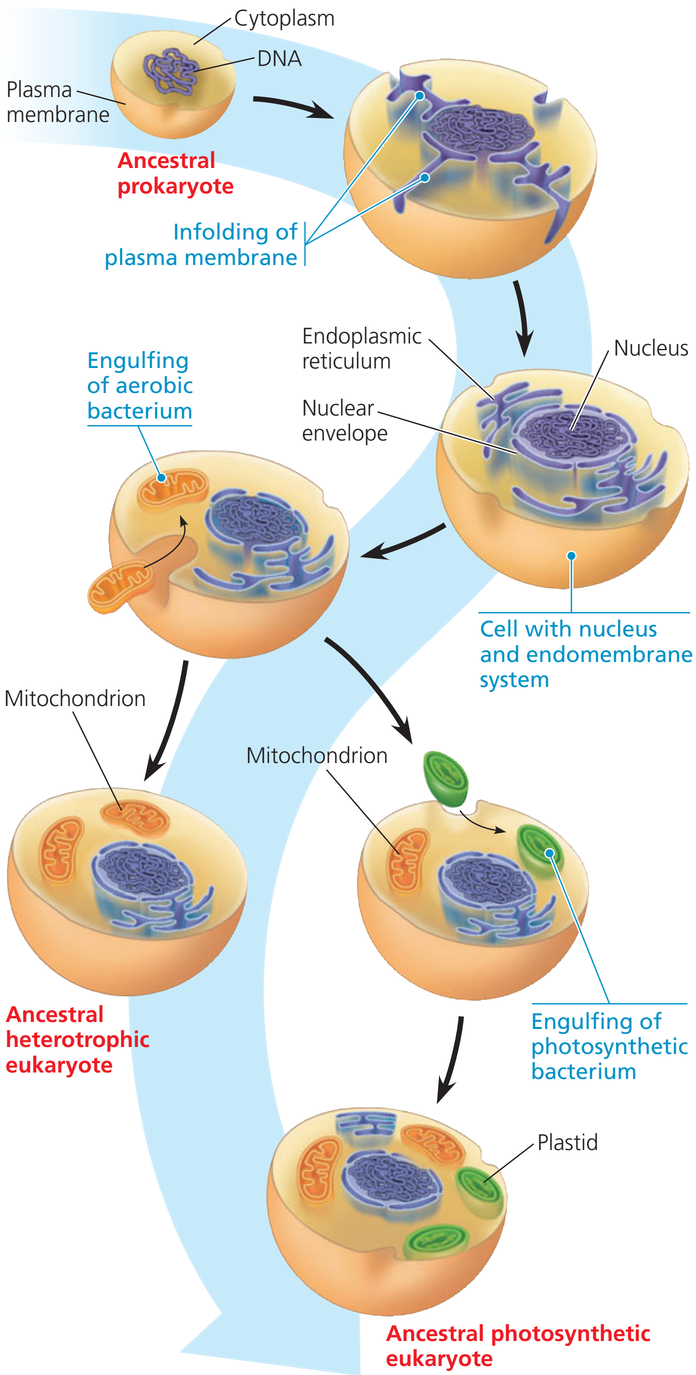
Origin of Mitochondria and Plastids

The idea that eukaryotes are "combination" organisms is related to the **endosymbiont theory**, which holds that mitochondria and plastids (a general term for chloroplasts and related organelles) were formerly small prokaryotes that began living within larger cells **(Figure 25.3)**. The term *endosymbiont* refers to a cell that lives within another cell, called the *host cell*. The prokaryotic ancestors of mitochondria and plastids probably gained entry to the host cell as undigested prey or internal parasites. Though such a process may seem unlikely, scientists have directly observed cases in which endosymbionts that began as prey or parasites came to have a mutually beneficial relationship with the host in as little as five years.

By whatever means the relationship began, we can hypothesize how the symbiosis could have become mutually beneficial. For example, in a world that was gradually becoming more 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. Thus, the **serial endosymbiosis** hypothesis

Table 25.1 Inferred Origins of Key Eukaryotic Features

Feature	Original Source
DNA replication enzymes	Archaeal
Transcription enzymes	Archaeal
Translation enzymes	Mostly archaeal
Cell division apparatus	Mostly archaeal
Endoplasmic reticulum	Archaeal and bacterial
Mitochondrion	Bacterial
Metabolic genes	Mostly bacterial



▲ **Figure 25.3 A hypothesis for the origin of eukaryotes through endosymbiosis.** The proposed host was an archaean or a cell descended from archaeal ancestors. The proposed ancestors of mitochondria were aerobic, heterotrophic prokaryotes, whereas those of plastids were photosynthetic prokaryotes. In this figure, the arrows represent change over evolutionary time.

supposes that mitochondria evolved before plastids through a sequence of endosymbiotic events (see Figure 25.3).

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 prokaryotes.
- Mitochondria and plastids replicate by a splitting process that is similar to that of certain prokaryotes. Mitochondria and plastids both contain 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 prokaryotic ribosomes than they are to the cytoplasmic ribosomes of eukaryotic cells.

Which prokaryotic lineages gave rise to mitochondria? To answer this question, researchers have compared the DNA sequences of mitochondrial genes (mtDNA) with those found in major clades of bacteria and archaea. 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 24.19). Researchers have also compared genome sequences of various alpha proteobacteria with the entire mtDNA sequences of animals, plants, fungi, and protists. Such studies indicate that eukaryotic mitochondria descended from a single common ancestor, suggesting that mitochondria arose only

Scientific Skills Exercise

Interpreting Comparisons of Genetic Sequences

Which Prokaryotes Are Most Closely Related to Mitochondria? The first eukaryotes acquired mitochondria by endosymbiosis: A host cell engulfed an aerobic prokaryote that persisted within the cytoplasm to the mutual benefit of both cells. In studying which living prokaryotes might be most closely related to mitochondria, researchers compared ribosomal RNA (rRNA) sequences. Because most cells contain thousands of ribosomes, rRNA is the most abundant form of RNA in living cells and is suitable for comparing even distantly related species. In this exercise, you'll interpret some of their results to draw conclusions about the phylogeny of mitochondria.

How the Research Was Done Researchers isolated and cloned nucleotide sequences from the gene that codes for the small-subunit rRNA molecule for six organisms: wheat (a plant) and five bacterial species.

- Wheat, used as the source of mitochondrial rRNA genes
- *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 Cloned rRNA gene sequences for the six organisms 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 composition. Any positions that were identical across the rRNA genes of all six organisms were omitted from this comparison matrix.

	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						–

Interpret the Data

1. First, make sure you understand how to read the comparison matrix. Find the cell that represents the comparison of *C. testosteroni* and *E. coli*. What value is given in this cell? What does that value signify about the comparable rRNA gene sequences in those two organisms? Explain why some cells have a dash rather than a value. 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. Which species of bacterium has an rRNA gene that is most similar to that of the wheat mitochondrion? What is the significance of this similarity?

Data from D. Yang, et al., Mitochondrial origins, *Proceedings of the National Academy of Sciences USA* 82:4443–4447 (1985).

MB A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

once over the course of evolution. Similar analyses indicate that plastids arose once from an engulfed cyanobacterium.

While the lineages that gave rise to mitochondria and plastids have been identified, questions remain about the identity of the host cell that engulfed an alpha proteobacterium. According to recent genomic studies, the host came from an archaeal lineage, but which lineage remains undetermined. Alternatively, the host could have been a member of a lineage that was related to, but had diverged from, its archaeal ancestors. In this case, the host may have been a "protoeukaryote" in which certain features of eukaryotic cells had evolved, such as an endomembrane system and a cytoskeleton that enabled it to change shape (and thereby engulf the alpha proteobacterium).

Plastid Evolution: A Closer Look

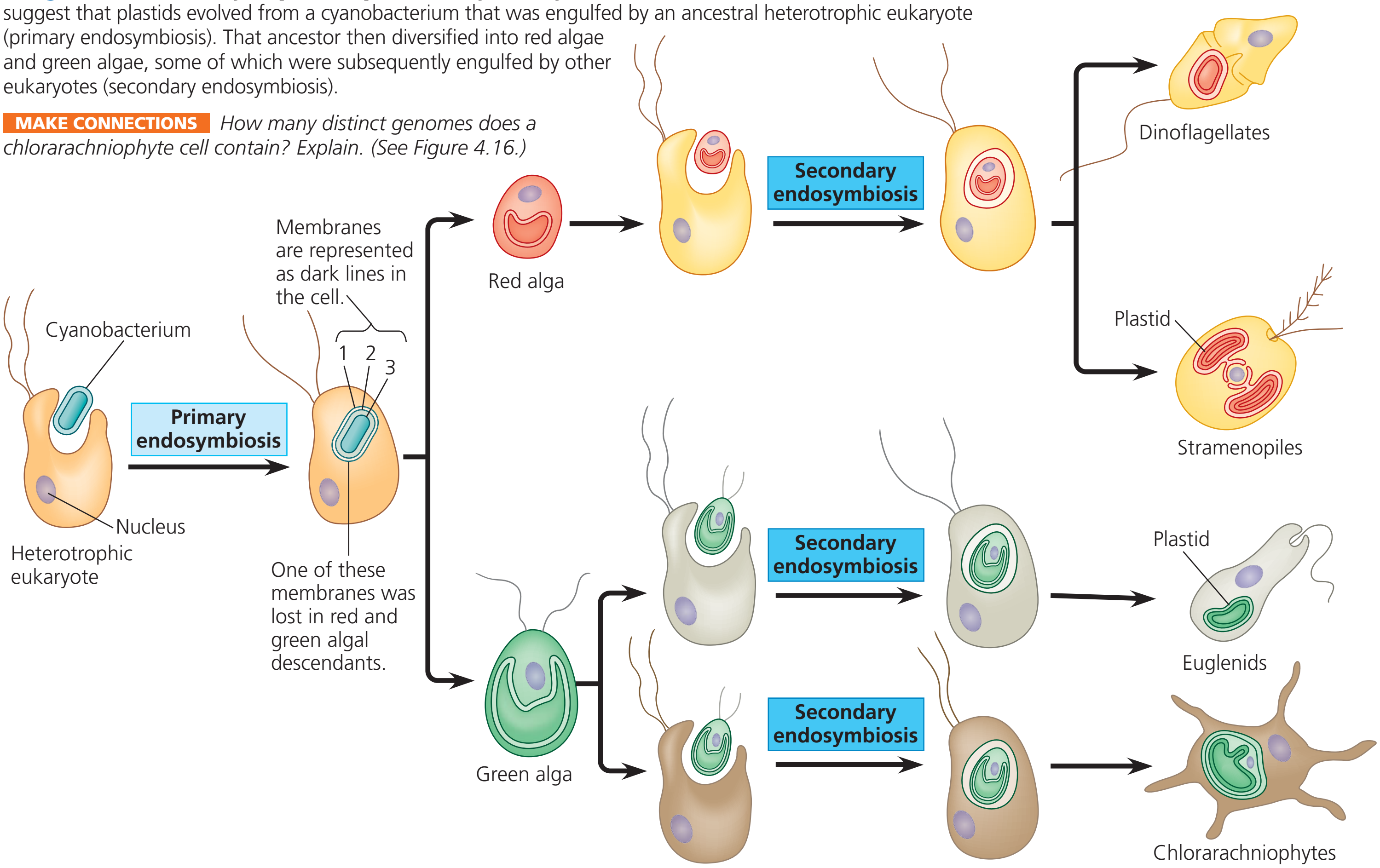
As you've seen, current evidence indicates that mitochondria are descended from a bacterium that was engulfed by a cell from an archaeal lineage. This event gave rise to the eukaryotes. There is also much evidence that later in eukaryotic history, a lineage of heterotrophic eukaryotes acquired an additional endosymbiont—a photosynthetic cyanobacterium—that then evolved into plastids. According to the hypothesis illustrated in **Figure 25.4**, this plastid-bearing lineage gave rise to two lineages of photosynthetic protists, red algae and green algae.

Let's examine some of the steps shown in Figure 25.4 in more detail. 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 24.7). 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**: They were ingested in the food vacuoles of heterotrophic eukaryotes and became endosymbionts themselves. For example, as shown in Figure 25.4, protists known as chlorarachniophytes likely evolved when a heterotrophic eukaryote engulfed a green alga. Evidence for this process can be found within the engulfed cell, which contains a tiny vestigial nucleus, called a *nucleomorph*. Genes from the nucleomorph are still transcribed, and their DNA sequences indicate that the engulfed cell was a green alga. Also consistent with the hypothesis that chlorarachniophytes evolved from a eukaryote that engulfed another eukaryote, their plastids are surrounded by *four* membranes. The two inner membranes originated as the inner and

▼ **Figure 25.4 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).

MAKE CONNECTIONS *How many distinct genomes does a chlorarachniophyte cell contain? Explain. (See Figure 4.16.)*



outer membranes of the ancient cyanobacterium; the third membrane is derived from the engulfed alga's plasma membrane; and the outermost membrane is derived from the heterotrophic eukaryote's food vacuole.

CONCEPT CHECK 25.1

1. Describe major events in the evolution of early eukaryotes that are documented in the fossil record.
2. Explain why eukaryotes are said to be "combination" organisms, and summarize the role of endosymbiosis in eukaryotic evolution.
3. **WHAT IF?** Suppose the photosynthetic organelle of a protist is discovered to be most closely related to a different cyanobacterium than the one that gave rise to plastids. What would this result suggest about the origin of eukaryotic photosynthesis?

For suggested answers, see Appendix A.

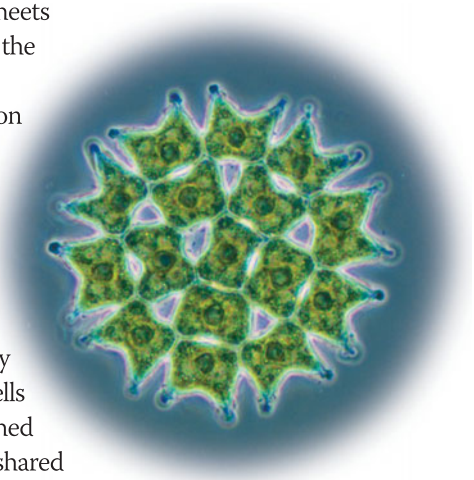
CONCEPT 25.2

Multicellularity has originated several times in eukaryotes

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. This burst of evolutionary change resulted in the immense variety of unicellular protists 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.

Multicellular Colonies

The first multicellular forms were *colonies*, collections of cells that are connected to one another but show little or no cellular differentiation. Multicellular colonies consisting of simple filaments, balls, or cell sheets occur early and often in the eukaryotic fossil record, and they remain common today **(Figure 25.5)**. Such simple colonies are often found in eukaryotic lineages whose members have rigid cell walls. In such organisms, a colony may take shape as the cells divide and remain attached to one another by their shared cell walls. Simple colonies are also found in eukaryotes that lack rigid cell walls, but in this case a colony may form when dividing cells are held together by proteins that physically connect adjacent cells to one another.



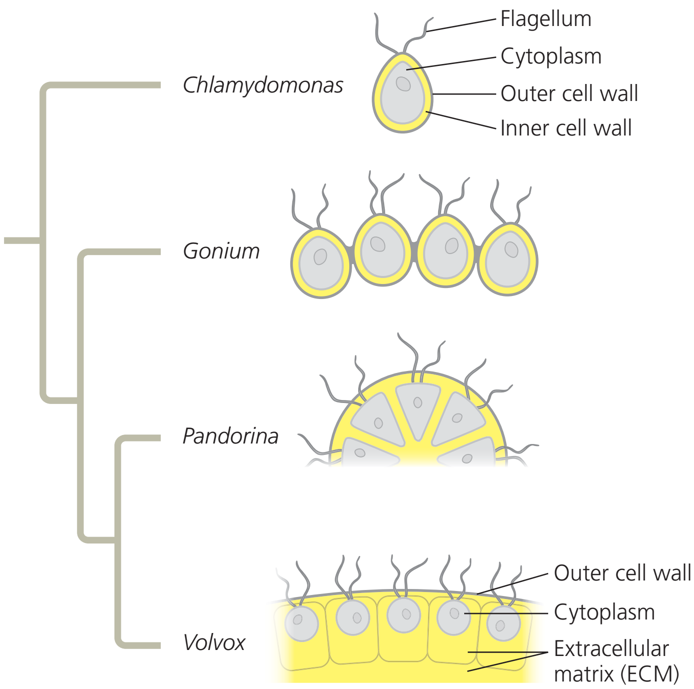
▲ **Figure 25.5** ***Pediastrum.*** This photosynthetic eukaryote forms flat colonies (LM).

Some simple colonies have features that are intermediate between those of single-celled eukaryotes and those of more complex multicellular forms, such as plants, fungi, and animals. As you'll see in the following sections, such differences between unicellular, colonial, and multicellular eukaryotes can reveal clues to the origin of multicellularity.

Independent Origins of Complex Multicellularity

Although they occur in fewer lineages than do simple colonies, multicellular organisms with differentiated cells originated multiple times over the course of eukaryotic evolution. Examples include lineages of red, green, and brown algae, as well as plants, fungi, and animals. Genetic and morphological data indicate that these different lineages of complex multicellular eukaryotes arose independently of one another. For example, although both fungi and animals arose from single-celled ancestors, they arose from *different* single-celled ancestors.

The fact that complex multicellularity has originated multiple times allows us to examine the similarities and differences in how these independent groups arose. We'll begin with *Volvox*, a multicellular green alga with two types of differentiated cells **(Figure 25.6)**. (It is because of these differentiated cells that most researchers refer to *Volvox* as "multicellular," as opposed to "colonial.") DNA evidence indicates that this



▲ **Figure 25.6 Morphological change in the *Volvox* lineage.** *Chlamydomonas* cell wall has both an outer wall (gray) and an inner wall (yellow). *Gonium* cells resemble a *Chlamydomonas* cell, and the structures that attach *Gonium* cells to one another contain proteins homologous to those in the *Chlamydomonas* cell wall. In *Pandorina* and *Volvox*, the cells are embedded in an extracellular matrix containing proteins homologous to those found in the *Chlamydomonas* inner wall.

species forms a monophyletic group with a single-celled alga (*Chlamydomonas*) and several colonial species. *Volvox* cells are embedded in an extracellular matrix composed of proteins homologous to those in the *Chlamydomonas* cell wall; the same is true for the colonial species that branch between *Chlamydomonas* and *Volvox*. This suggests that multicellularity in *Volvox* may have originated as descendants of a single-celled common ancestor gave rise to a series of larger and more complex colonial forms.

A 2010 comparison of the *Chlamydomonas* and *Volvox* genomes yielded a further surprising result: *Volvox* has few novel genes that could account for the differences in morphology seen between these species. This suggests that the transition to multicellularity may not require the origin of many new genes. Instead, this transition may result from changes in how existing genes are used—a conclusion that is also supported by recent studies on the origin of multicellularity in animals.

Steps in the Origin of Multicellular Animals

Although the origin of animals was a pivotal moment in the history of life, until recently little was known about the genetic toolkit that facilitated the emergence of multicellular animals from their single-celled ancestors. One way to gather information about this toolkit is to identify protist groups that are closely related to animals. As shown in **Figure 25.7**, a combination of morphological and molecular evidence points 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 unicellular suspension feeder that resembled present-day choanoflagellates.

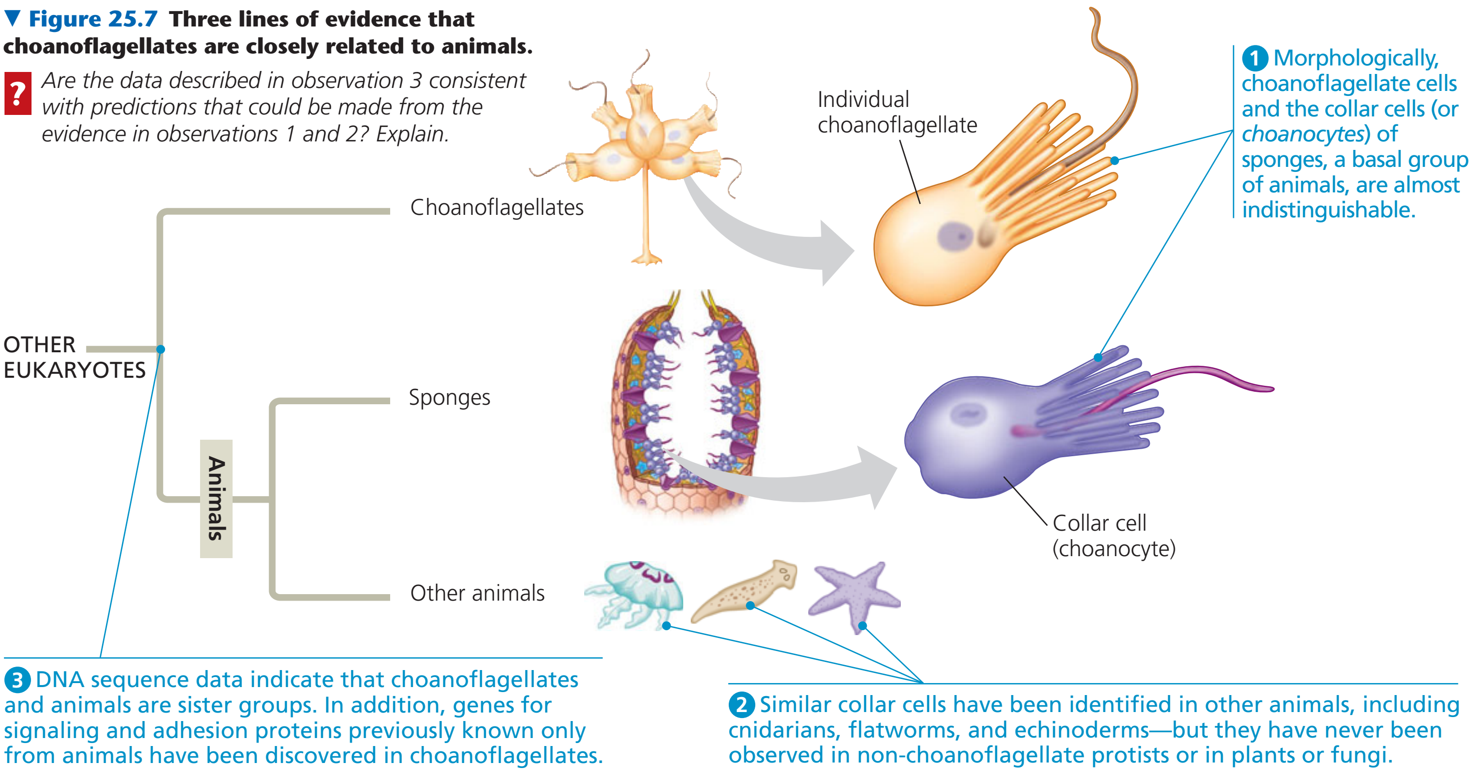
Note that the origin of multicellularity in animals required the evolution of new ways for cells to adhere (attach) and signal (communicate) to each other. In an effort to learn more about such mechanisms, a recent study compared the genome of the unicellular choanoflagellate *Monosiga brevicollis* with those of representative animals.

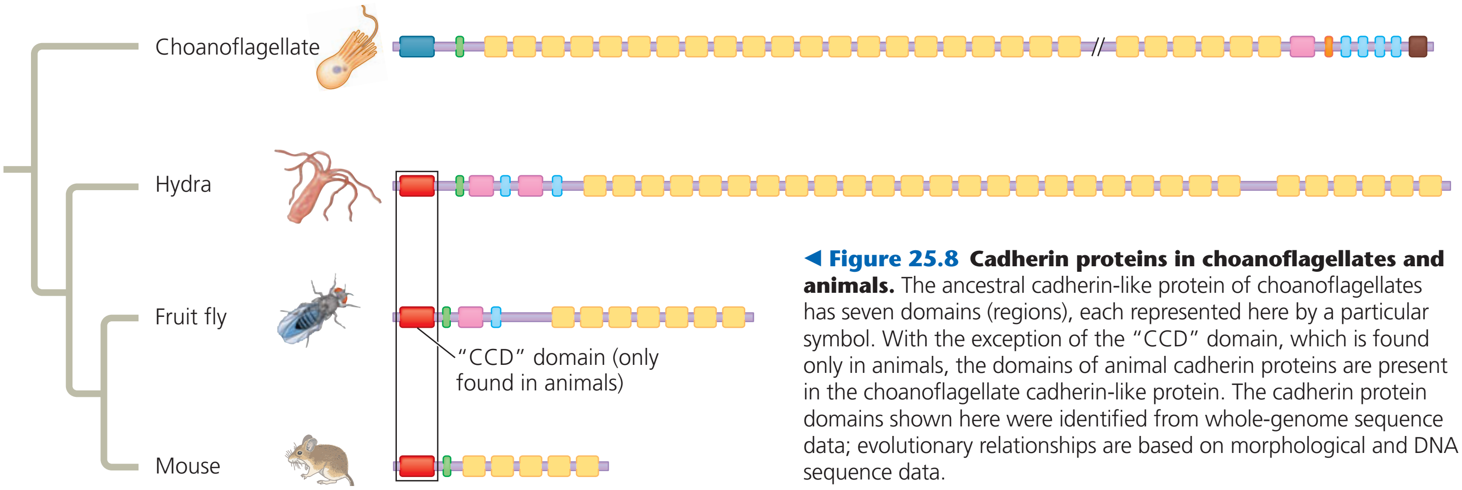
This analysis uncovered 78 protein domains in *M. brevicollis* that were otherwise only known to occur in animals. (A *domain* is a key structural or functional region of a protein.) In animals, many of these shared protein domains function in cell adherence or cell signaling. To give just two examples, *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.

New research has also enabled us to take a closer look at specific proteins that played important roles in the origin of multicellularity in animals. Were these proteins composed mostly of domains found in ancestral choanoflagellate proteins? Or did they have a more novel structure? Consider the cadherin attachment proteins mentioned earlier. 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 25.8)**. However, animal cadherin proteins that attach cells to one another also contain a highly conserved region not found in

▼ **Figure 25.7 Three lines of evidence that choanoflagellates are closely related to animals.**

? *Are the data described in observation 3 consistent with predictions that could be made from the evidence in observations 1 and 2? Explain.*





◀ **Figure 25.8 Cadherin proteins in choanoflagellates and animals.** The ancestral cadherin-like protein of choanoflagellates has seven 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 choanoflagellate protein (the "CCD" domain shown in Figure 25.8). These results suggest that the origin of the cadherin attachment protein occurred by the rearrangement of protein domains found in choanoflagellates—along with the incorporation of a novel domain, the conserved CCD region.

Overall, comparisons of choanoflagellate and animal genome sequences tell us 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. Thus, as we also saw for the origin of multicellularity in *Volvox*, the origin of multicellularity in animals may have resulted mostly from the co-opting of genes used for other purposes in choanoflagellates—not from the evolution of a genetic toolkit composed of many novel genes.

CONCEPT CHECK 25.2

1. Summarize the evidence that choanoflagellates are the sister group of animals.
2. **MAKE CONNECTIONS** Describe how the origin of multicellularity in animals illustrates Darwin's concept of descent with modification (see Concept 19.2).
3. **WHAT IF?** Cells in *Volvox*, plants, and fungi are similar in being bounded by a cell wall. Predict whether the cell-to-cell attachments of these organisms form using similar or different molecules. Explain.

For suggested answers, see Appendix A.

CONCEPT 25.3

Four "supergroups" of eukaryotes have been proposed based on morphological and molecular data

How have events described so far in this chapter influenced the diversity of eukaryotes living today? First, by their very nature, eukaryotes are "combination" organisms. Having originated by endosymbiosis, they had archaeal and bacterial genes and they possessed endosymbionts with novel metabolic capabilities. These features promoted the diversification of unicellular protists seen in the fossil record and still evident today in a drop of pond water. The independent origins of complex multicellularity in several eukaryotic lineages also had a major influence. Each of these independent groups evolved different solutions to the various challenges that all organisms face, thus contributing to the rich diversity of eukaryotes alive today. We'll survey that diversity here, beginning with an overview of the big picture: the four eukaryotic "supergroups."

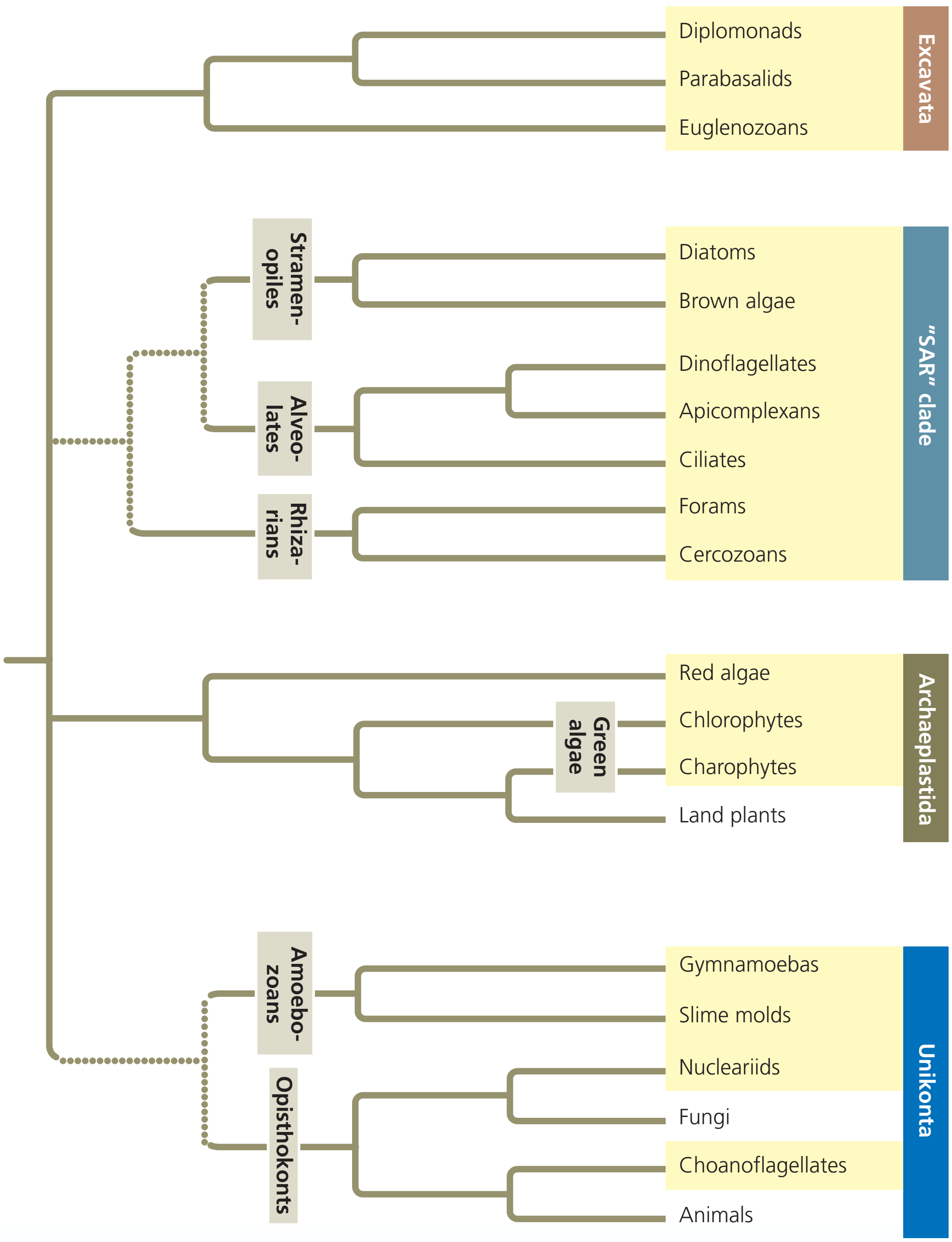
Four Supergroups of Eukaryotes

Our understanding of the evolutionary history of eukaryotes has been in a state of flux in recent years. 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 lineages of protists are now recognized as kingdoms in their own right. Other hypotheses have been discarded as well. For example, in the early 1990s, many biologists thought that the oldest lineage of living eukaryotes consisted of the *amitochondriate protists*, organisms without conventional mitochondria. 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 eukaryotes 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 25.9**. Because the root of the eukaryotic tree is not

▼ Figure 25.9 Exploring Eukaryotic Diversity

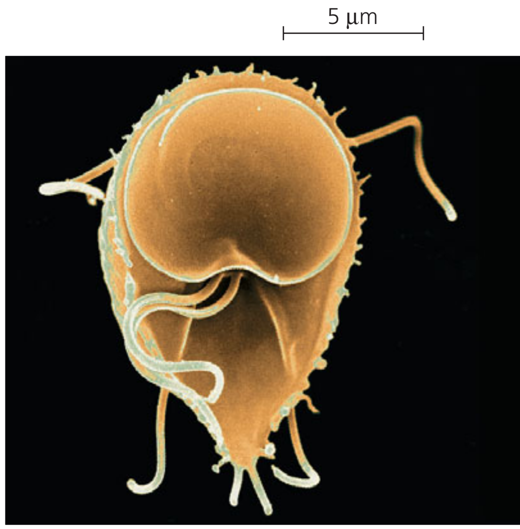
The tree below represents a phylogenetic hypothesis for the relationships among eukaryotes on Earth today. The eukaryotic groups at the branch tips are related in larger "supergroups," labeled vertically at the far right of the tree. Groups that were formerly classified in the kingdom Protista are highlighted in yellow. Dotted lines indicate evolutionary relationships that are uncertain and proposed clades that are under active debate. 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.



? *Based on the fossil record of early eukaryotes and the tree shown here, by what date had the supergroups begun to diverge from one another? Explain.*

Excavata

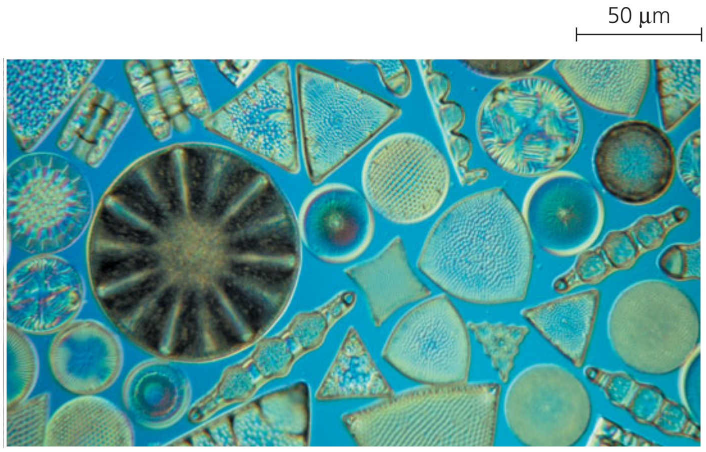
Some members of this supergroup have an "excavated" groove on one side of the cell body. Two major clades (the parabasalids and diplomonads) have modified mitochondria; members of a third clade (the euglenozoans) have flagella that differ in structure from those of other organisms. Excavates include 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.

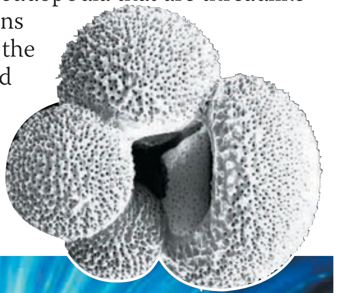
"SAR" Clade

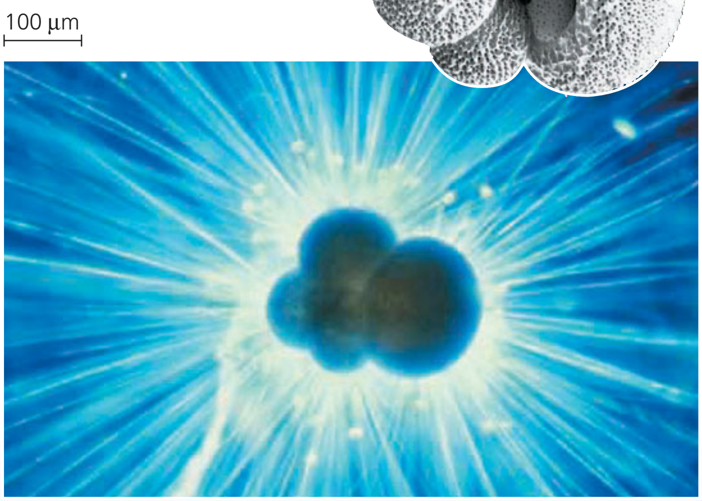
This supergroup contains (and is named after) three large and very diverse clades: Stramenopila, Alveolata, and Rhizaria. Stramenopiles include some of the most important photosynthetic organisms on Earth, such as the diatoms shown here. Alveolates also include photosynthetic species, as well as important pathogens, such as *Plasmodium*, which causes malaria. Many of the key groups of photosynthetic stramenopiles and alveolates are thought to have arisen by secondary endosymbiosis.



Diatom diversity. These beautiful single-celled protists are important photosynthetic organisms in aquatic communities (LM).

The rhizarian subgroup of the SAR clade 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.

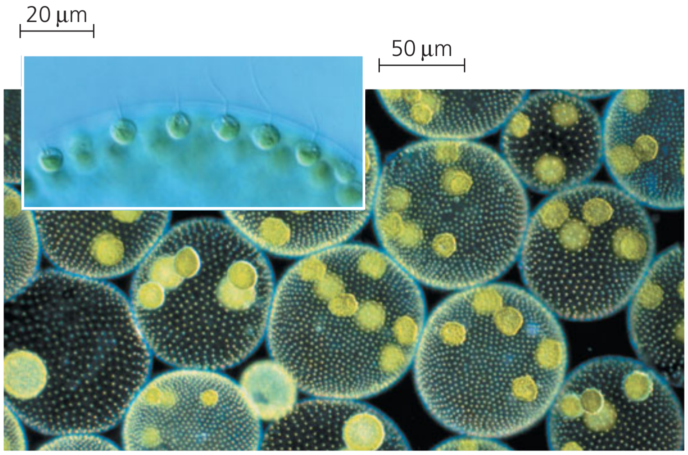




***Globigerina*, a rhizarian in the SAR supergroup.** This species is a foram, a group whose members have threadlike pseudopodia that extend through pores in the shell, or test (LM). The inset shows a foram test, which is hardened by calcium carbonate.

Archaeplastida

This supergroup of eukaryotes includes red algae and green algae, along with land 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 resembles a hollow ball whose wall is composed of hundreds of biflagellated cells (see inset LM) embedded in a gelatinous matrix. The cells in the wall are usually connected by cytoplasmic strands; 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).

Unikonta

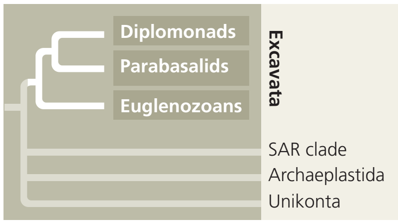
This supergroup of eukaryotes includes amoebas that have lobe- or tube-shaped pseudopodia, as well as animals, fungi, and non-amoeba protists that are closely related to animals or fungi. According to one current hypothesis, the unikonts may have been the first group of eukaryotes to diverge from other eukaryotes; however, this hypothesis has yet to be widely accepted.

A unikont amoeba. This amoeba, the gymnamoeba *Amoeba proteus,* is using its pseudopodia to move.

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 organisms were the first to diverge from the others. In addition, while some of the groups in Figure 25.9 are well supported by morphological and DNA data, others are more controversial.

We'll now examine some representative members of the four supergroups. As you read about these groups, it may be helpful to focus less on the specific names of their members and more on why these organisms are important and how ongoing research is elucidating their evolutionary relationships.

Excavates



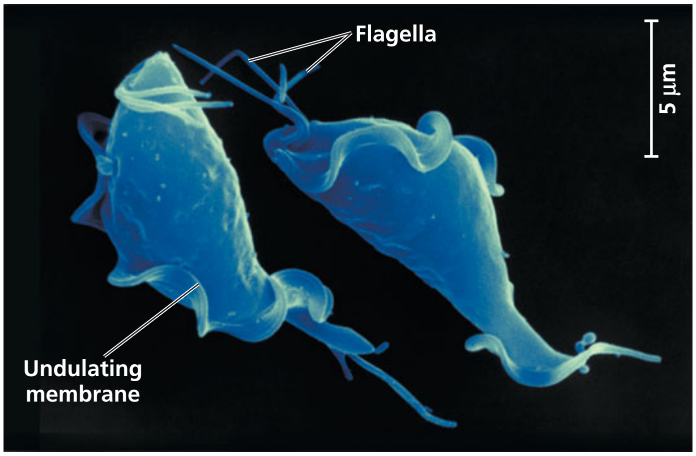
The clade **Excavata** (the excavates) was originally proposed based on morphological studies of the cytoskeleton. The name derives from the fact that some members of this diverse group feature an "excavated" feeding groove on one side of the cell body. The excavates include the diplomonads, the parabasalids, and the euglenozoans. Molecular data indicate that each of these three groups is monophyletic, and recent genomic studies have supported the monophyly of the excavate supergroup.

Diplomonads and Parabasalids

The protists in these two groups lack plastids and have highly modified 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 25.9). These parasites propel themselves within a host using multiple flagella.

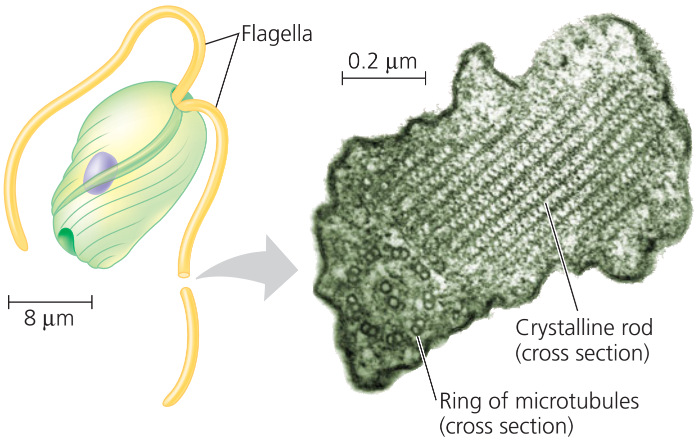
Parabasalids also have reduced mitochondria; called *hydrogenosomes*, these organelles generate some energy anaerobically, releasing hydrogen gas as a by-product. The best-known parabasalid is *Trichomonas vaginalis*, a sexually transmitted parasite that infects some 5 million people each year. *T. vaginalis* 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 25.10)**.



▲ **Figure 25.10 The parabasalid parasite, *Trichomonas vaginalis* (colorized SEM).**

Euglenozoans

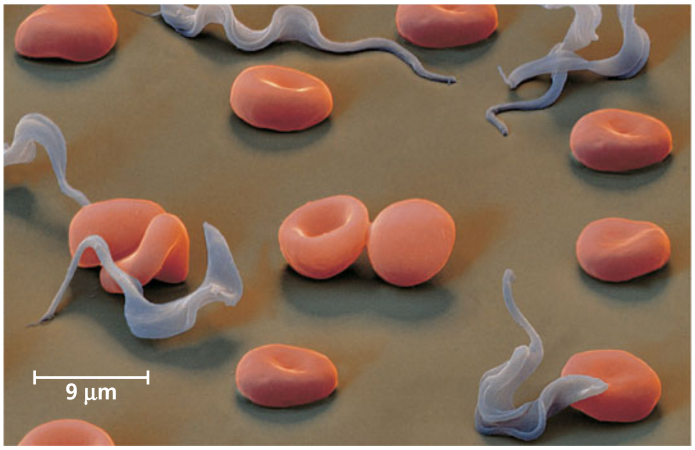
Protists called **euglenozoans** belong to a diverse clade that includes predatory heterotrophs, photosynthetic autotrophs, and parasites. The main morphological feature that distinguishes protists in this clade is the presence of a rod with either a spiral or a crystalline structure inside each of their flagella **(Figure 25.11)**. The two best-studied groups of euglenozoans are the euglenids and the kinetoplastids.



▲ **Figure 25.11 Euglenozoan flagellum.** Most euglenozoans have a crystalline rod inside one of their flagella (the TEM is a flagellum shown in cross section).

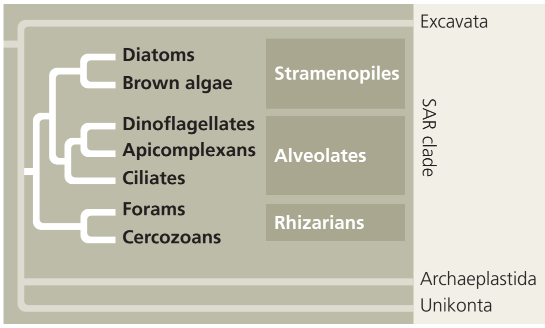
A *euglenid* has a pocket at one end of the cell from which one or two flagella emerge (see the drawing in Figure 25.11). Some euglenids perform photosynthesis when sunlight is available; when sunlight is not available, they can become heterotrophic, absorbing organic nutrients from their environment. Many other euglenids engulf prey by phagocytosis.

A *kinetoplastid* has a single, large mitochondrion that contains an organized mass of DNA called a kinetoplast. These protists include species that feed on prokaryotes in aquatic 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, a neurological disease that is invariably fatal if not treated **(Figure 25.12)**.



▲ **Figure 25.12** ***Trypanosoma*, the kinetoplastid that causes sleeping sickness.** The purple, ribbon-shaped cells among these red blood cells are the trypanosomes (colorized SEM).

The "SAR" Clade



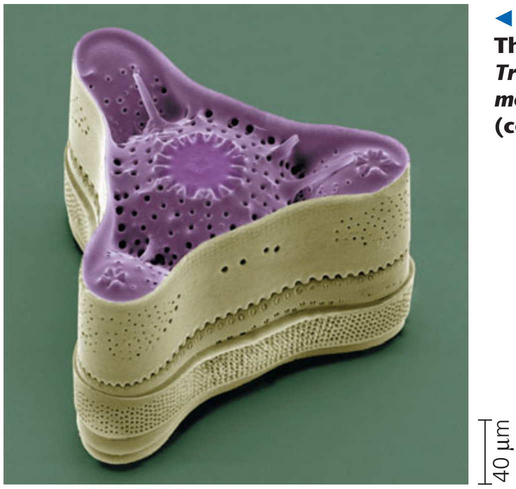
Recent genomic studies have led researchers to propose that three major clades of protists—the stramenopiles, alveolates, and rhizarians—form a monophyletic supergroup referred to as the **"SAR" clade**, after the first letters of its member clades.

Stramenopiles

One major subgroup of the SAR clade, the **stramenopiles**, arose by secondary endosymbiosis (see Figure 25.4) and include some of the most important photosynthetic organisms on the planet. Here we'll focus on two clades of stramenopiles: diatoms and brown algae.

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 25.13)**. 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. 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. As we'll

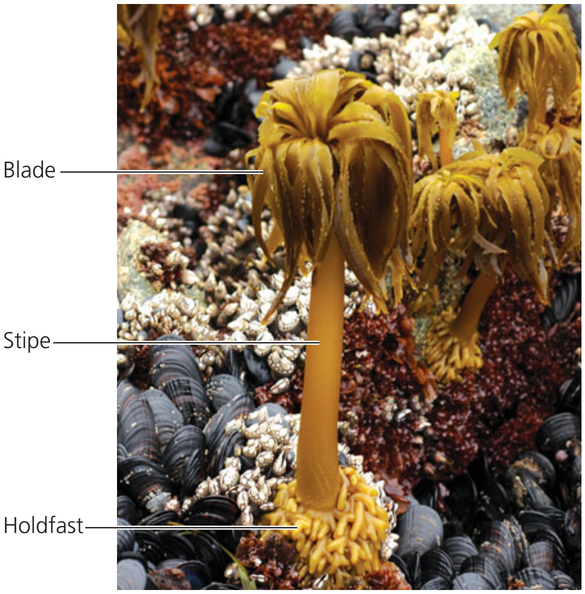


◀ **Figure 25.13 The diatom *Triceratium morlandii* (colorized SEM).**

discuss later in the chapter, the photosynthetic activity of these widespread and abundant algae can affect global carbon dioxide levels.

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, where the water is cool. 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 tissues and organs that resemble those in plants, such as a rootlike **holdfast**, which anchors the alga, and a stemlike **stipe**, which supports the leaflike **blades (Figure 25.14)**. However, morphological and DNA evidence show that these

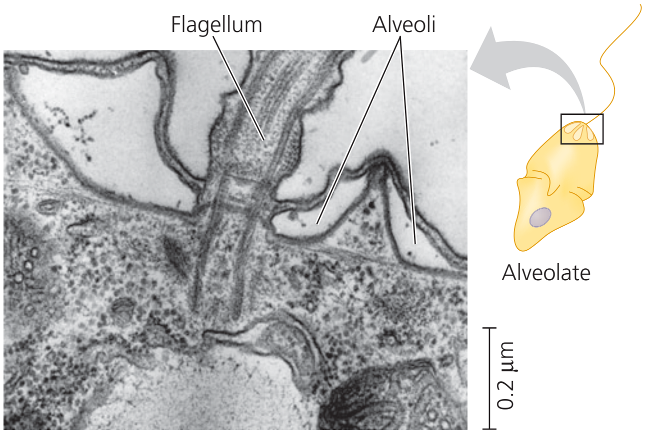


▲ **Figure 25.14 Seaweeds: adapted to life at the ocean's margins.** The sea palm (*Postelsia*) lives on rocks along the coast of the northwestern United States and western Canada. The body of this brown alga is well adapted to maintaining a firm foothold despite the crashing surf.

similarities evolved 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 use a different means: Their blades are attached to stipes that can rise as much as 60 m from the seafloor, more than half the length of a football field.

Alveolates

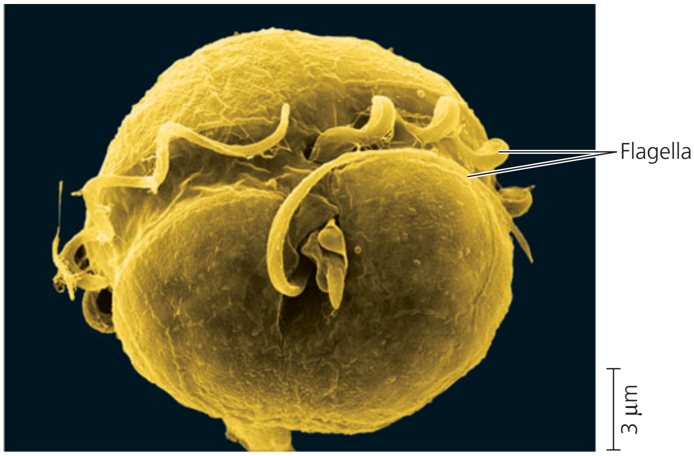
Members of the next subgroup of the SAR clade, the **alveolates**, have membrane-enclosed sacs (alveoli) just under the plasma membrane **(Figure 25.15)**. Alveolates are abundant in many habitats and include a wide range of photosynthetic and heterotrophic protists. We'll discuss two alveolate clades here, a group of flagellates (the dinoflagellates) and a group of protists that move using cilia (the ciliates); we'll discuss a third clade (the apicomplexans) that parasitizes animals in Concept 25.4.



▲ **Figure 25.15 Alveoli.** These sacs under the plasma membrane are a characteristic that distinguishes alveolates from other eukaryotes (TEM).

Dinoflagellates The cells of many **dinoflagellates** are reinforced by cellulose plates. Two flagella located in grooves in this "armor" make dinoflagellates (from the Greek *dinos*, whirling) spin as they move through the waters of their marine and freshwater communities **(Figure 25.16)**. Although the group originated by secondary endosymbiosis (see Figure 25.4), roughly half of all dinoflagellates are now purely heterotrophic. Others are important photosynthetic species, while still others are **mixotrophs**, organisms that combine photosynthesis *and* heterotrophic nutrition.

Episodes of explosive population growth, or *blooms*, in dinoflagellates sometimes cause a phenomenon called "red tide." The blooms make coastal waters appear brownish red or pink because of the presence of carotenoids, the most common pigments in dinoflagellate plastids. Toxins produced by certain



▲ **Figure 25.16 *Pfiesteria shumwayae*, a dinoflagellate.** Beating of the spiral flagellum, which lies in a groove that encircles the cell, makes this alveolate spin (colorized SEM).

dinoflagellates have caused massive kills of invertebrates and fishes. Humans who eat molluscs that have accumulated the toxins are affected as well, sometimes fatally.

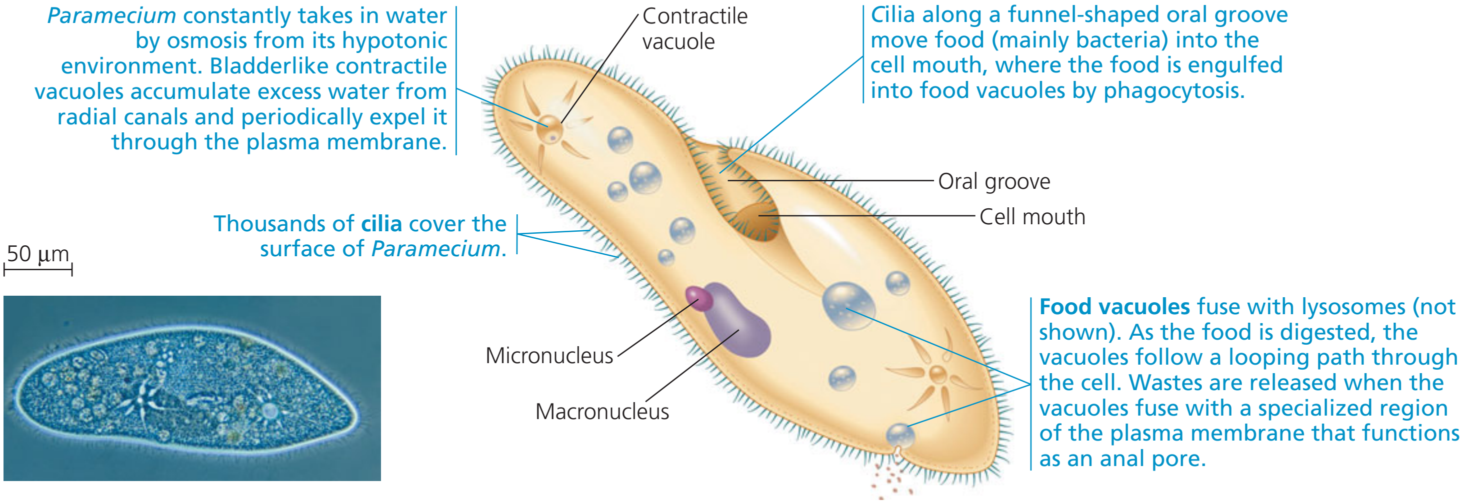
Ciliates The **ciliates** are a large and varied group of protists named for their use of cilia to move and feed **(Figure 25.17)**. Most ciliates are predators, typically of bacteria or small protists (see Figure 25.1). The cilia may completely cover the cell surface or may be clustered in a few rows 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.

Rhizarians

Our next subgroup of the SAR clade is the **rhizarians**. Many species in this group are **amoebas**, protists that move and feed by means of **pseudopodia**, extensions that may bulge from almost anywhere on the cell surface. An amoeba moves by extending a pseudopodium and anchoring the 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 (nonamoeboid) protists that feed using threadlike pseudopodia.

We'll examine two groups of rhizarians here: forams and cercozoans.

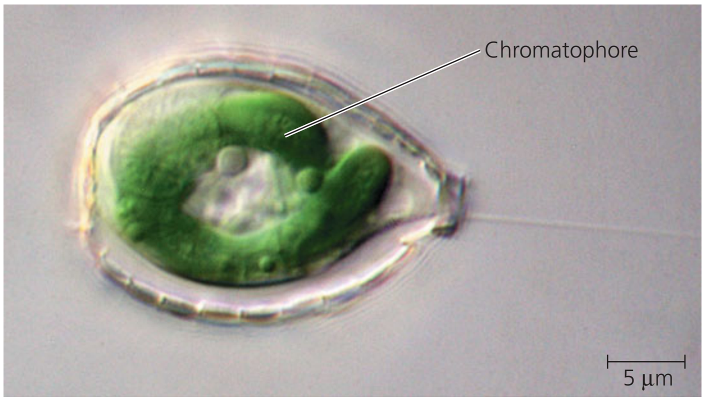
Forams The protists called **foraminiferans** (from the Latin *foramen*, little hole, and *ferre*, to bear), or **forams**, are named for their porous shells, called **tests** (see Figure 25.9). Foram tests consist of a single piece of organic material that is hardened with calcium carbonate in most species. 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



▲ **Figure 25.17 Structure and function in the ciliate *Paramecium caudatum*.**

the tests. Found in both lakes and oceans, most forams live in sand or attach themselves to rocks or algae, but some drift in currents near the water's surface. The largest forams, though single-celled, have tests with a diameter of several centimeters.

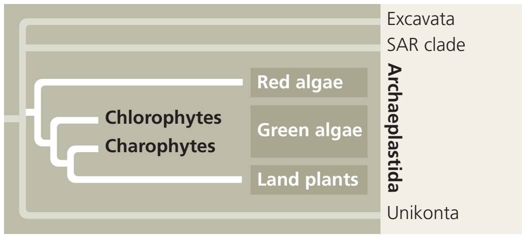
Cercozoans First identified in molecular phylogenies, the **cercozoans** are a large group of amoeboid and flagellated protists that feed with threadlike pseudopodia. Common in marine, freshwater, and soil ecosystems, many cercozoans are parasites of plants, animals, or other protists; many others are predators that feed on bacteria, fungi, and other protists. 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 carbon dioxide. As described in **Figure 25.18**,



▲ **Figure 25.18 A second case of primary endosymbiosis?** The cercozoan *Paulinella* conducts photosynthesis in a unique sausage-shaped structure called a chromatophore (LM). Chromatophores are surrounded by a membrane with a peptidoglycan layer, suggesting that they are derived from a bacterium. DNA evidence indicates that chromatophores are derived from a different cyanobacterium than that from which other plastids are derived.

Paulinella appears to represent an intriguing additional evolutionary example of a eukaryotic lineage that obtained its photosynthetic apparatus directly from a cyanobacterium.

Archaeplastids



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 25.4), and the lineage that produced green algae then gave rise to land plants. Together, red algae, green algae, and land plants make up our third eukaryotic supergroup, which is called **Archaeplastida**. We will examine plants and the colonization of land in Chapter 26; 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 a photosynthetic pigment called phycoerythrin, which masks the green of chlorophyll. However, other species (those adapted to more 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 function heterotrophically as parasites on other red algae.

▶ ***Bonnemaisonia hamifera.*** This red alga has a filamentous form.

▼ **Nori.** The red alga *Porphyra* has a leafy form and is the source of a traditional Japanese food.

The seaweed is grown on nets in shallow coastal waters.

After being dried, the paper-thin, glossy sheets of nori make a mineral-rich wrap for rice, seafood, and vegetables in sushi.

▲ **Figure 25.19 Red algae.**

Red algae are the most abundant large algae 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—one species of red alga has been discovered near the Bahamas at a depth of more than 260 m. Most red algae are multicellular, and they grow in a variety of forms **(Figure 25.19)**. 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. Red algae reproduce sexually. 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 land plants. Molecular systematics and cellular morphology leave little doubt that green algae and land 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.

(a) *Ulva,* or sea lettuce. This edible chlorophyte has leaflike blades and a holdfast that anchors the alga.

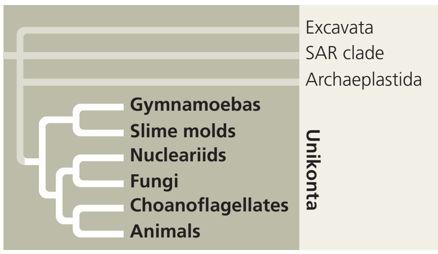
(b) *Caulerpa,* an intertidal chlorophyte. The filaments lack cross-walls and thus are multinucleate. In effect, the algal body is one huge "supercell."

▲ **Figure 25.20 Multicellular chlorophytes.**

Green algae are divided into two main groups, the charophytes and the chlorophytes. The charophytes are the algae most closely related to land plants, and we will discuss them along with plants in Chapter 26.

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. Nearly all species of chlorophytes reproduce sexually by means of biflagellated gametes that have cup-shaped chloroplasts. The simplest chlorophytes are unicellular species such as *Chlamydomonas* (see Figure 25.6), which resemble gametes of more complex chlorophytes. Some unicellular chlorophytes live independently in aquatic habitats while others live symbiotically within other eukaryotes, contributing part of their photosynthetic output to the food supply of their hosts. Larger size and greater complexity are found in various multicellular chlorophytes, including *Volvox* (see Figure 25.9) and *Ulva* **(Figure 25.20)**.

Unikonts



The fourth supergroup, **Unikonta**, is an extremely diverse group that includes animals, fungi, and some protists. There are two major clades of unikonts, the amoebozoans (gymnamoebas and slime molds) and the opisthokonts (animals, fungi, and closely related protist groups). Each of these two major clades is strongly supported by molecular systematics. The close relationship between amoebozoans and opisthokonts is more controversial. Support for this close relationship is provided by comparisons of myosin proteins and by some (but not all) studies based on hundreds of genes or whole genomes.

Another controversy 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 group of eukaryotes was the first to diverge from other eukaryotes. Some hypotheses, such as the amitochondriate hypothesis described earlier, have been abandoned, but researchers have yet to agree on an alternative. If the root of the eukaryotic tree were known, scientists could 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, some of which have produced conflicting results. Researchers have also tried a different approach based on tracing the occurrence of a rare evolutionary event **(Figure 25.21)**. Results from this "rare event" approach suggest that the unikonts were the first eukaryotes to diverge from other eukaryotes. If this hypothesis is correct, animals and fungi belong to an early-diverging group of eukaryotes, while protists that lack typical mitochondria (such as the diplomonads and parabasalids) diverged much later in the history of life. 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 thread-like pseudopodia found in rhizarians. Although some amoebozoans are parasites, most are free-living. The gymnamoebas, for example, are a group of free-living, unicellular predators and scavengers that are ubiquitous in soil and in aquatic environments (see Figure 25.9). Free-living amoebozoans also include the slime molds, a group of multicellular amoebozoans.

Slime molds were once thought to be fungi because, like fungi, they produce fruiting bodies that aid in spore dispersal. However, the resemblance between slime molds and fungi appears to be another case of evolutionary convergence. DNA sequence analyses indicate that slime molds descended from unicellular amoebozoan ancestors, making them another example of the independent evolution of multicellularity in eukaryotes (see Concept 25.2).

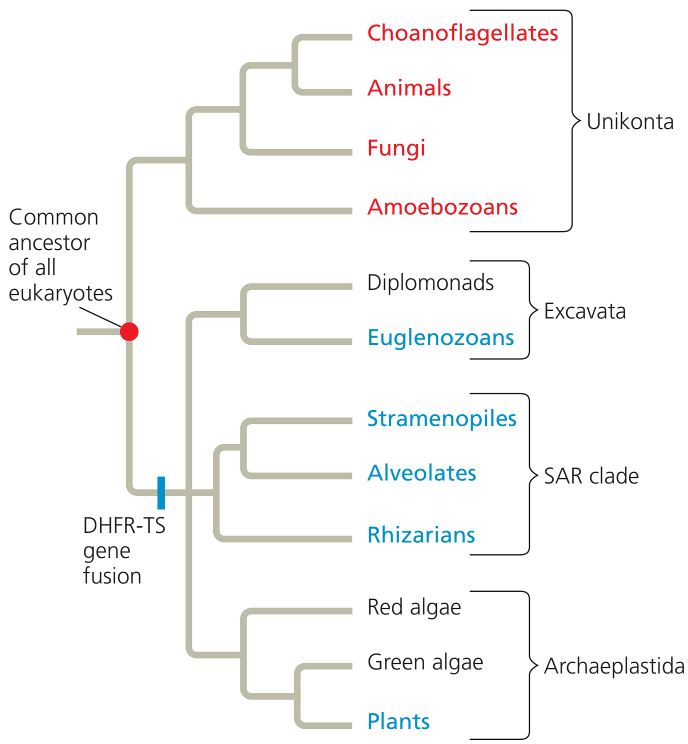
The life cycle of some slime molds can prompt us to question what it means to be an individual organism. Consider the cellular slime mold *Dictyostelium*. The feeding stage of this organism consists of solitary cells that function individually; but when food is depleted, the cells form an aggregate

▼ Figure 25.21 Inquiry

Where is the root of the eukaryotic tree?

Experiment Responding to the difficulty in determining the root of the eukaryotic phylogenetic tree, Alexandra Stechmann and Thomas Cavalier-Smith proposed a new approach. They studied two genes, one coding for the enzyme dihydrofolate reductase (DHFR), the other for the enzyme thymidylate synthase (TS). Their approach took advantage of a rare evolutionary event: In some organisms, the genes for DHFR and TS have fused, leading to the production of a single protein with both enzyme activities. Stechmann and Cavalier-Smith amplified (using PCR; see Figure 13.25) and sequenced the genes for DHFR and TS in nine species (one choanoflagellate; two amoebozoans; one euglenozoan; one stramenopile; one alveolate; and three rhizarians). They combined their data with previously published data for species of bacteria, animals, plants, and fungi.

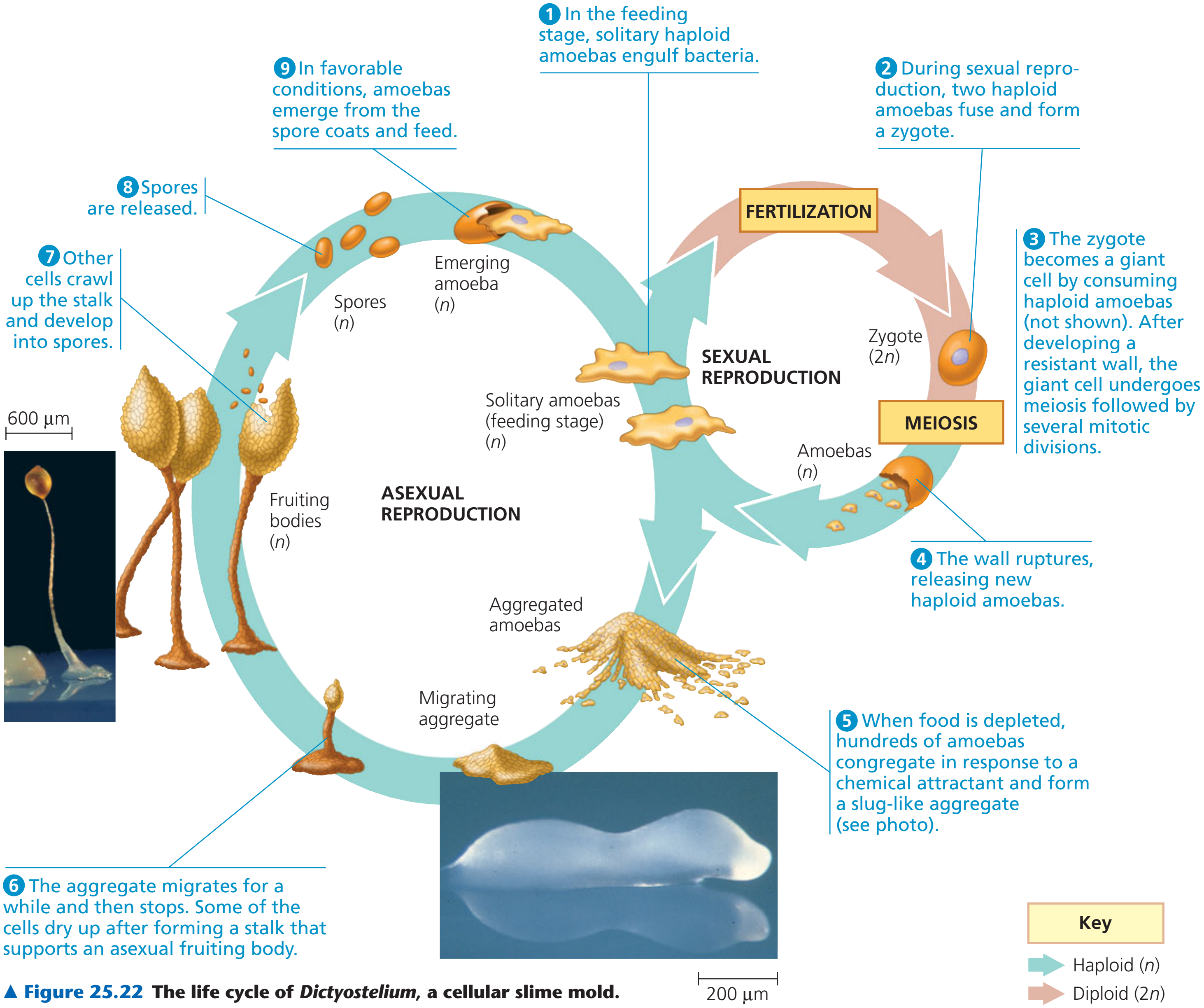
Results The bacteria studied all have separate genes coding for DHFR and TS, suggesting that this is the ancestral condition (red dot on the tree below). Other taxa with separate genes are denoted by red type. Fused genes are a derived character, found in certain members (blue type) of the supergroups Excavata, the SAR clade, and Archaeplastida:



Conclusion These results support the hypothesis that the root of the tree is located between the unikonts and all other eukaryotes, suggesting that the unikonts were the first group of eukaryotes to diverge. Because support for this hypothesis is based on only one trait—the fusion of the genes for DHFR and TS—more data are needed to evaluate its validity.

Source A. Stechmann and T. Cavalier-Smith, Rooting the eukaryote tree by using a derived gene fusion, *Science* 297:89–91 (2002).

WHAT IF? Stechmann and Cavalier-Smith wrote that their conclusions are "valid only if the genes fused just once and were never secondarily split." Why is this assumption critical to their approach?



▲ **Figure 25.22 The life cycle of *Dictyostelium*, a cellular slime mold.**

that functions as a unit **(Figure 25.22)**. These aggregated cells eventually form 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 disperse and later reproduce.

Opisthokonts

Opisthokonts are an extremely diverse group of eukaryotes that includes animals, fungi, and several groups of protists. We will discuss the colonization of land and the evolutionary history of fungi and animals in Chapters 26 and 27. Of the opisthokont protists, we will discuss the nucleariids in Chapter 26 because they are more closely related to fungi than they are to other protists. And as we discussed earlier in this chapter, the choanoflagellates 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 25.3

1. Briefly describe the organisms found in each of the four eukaryotic supergroups.
2. **MAKE CONNECTIONS** Review Figures 7.2 and 8.5. Summarize how CO_2 and O_2 are both used and produced by aerobic algae.
3. **WHAT IF?** DNA sequence data for a diplomonad, a euglenozoan, 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 25.9 did the mystery protist's lineage probably diverge from other eukaryotic lineages? Explain.

For suggested answers, see Appendix A.

CONCEPT 25.4

Single-celled eukaryotes play key roles in ecological communities and affect human health

As our survey of the four eukaryotic supergroups suggests, the large, multicellular organisms that we know best—the plants, animals, and fungi—are the tips of just a few branches on the eukaryotic tree of life. All the other branches are lineages of protists, and these protists exhibit an impressive range of structural and functional diversity, as we'll discuss. We'll then examine the effects of protists on ecological communities and human societies. (We focus on protists here, but we'll address similar topics for plants, fungi, and animals in Chapters 26 and 27.)

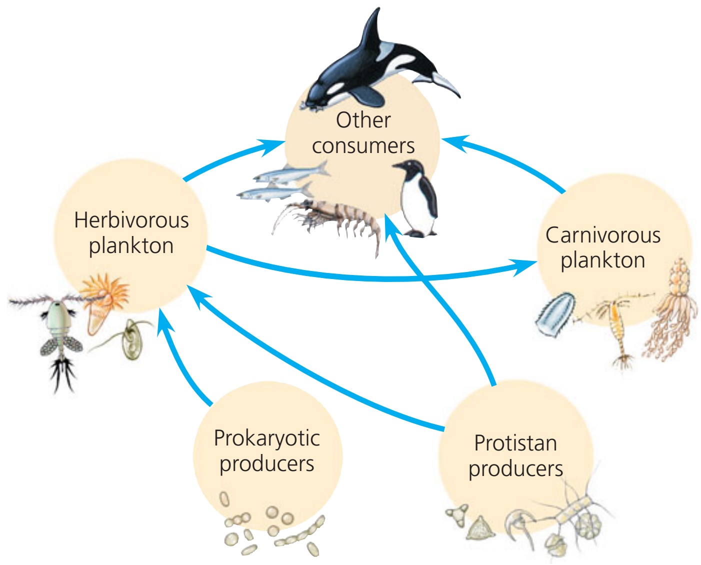
Structural and Functional Diversity in Protists

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 functions, but they do so using subcellular organelles, not multicellular organs: the nucleus, endoplasmic reticulum, Golgi apparatus, and lysosomes.

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 and lakes, many protists attach to the bottom or creep through the sand and silt, while others float near the water's surface. The protists living in these varied habitats also show a wide range of nutritional diversity. As we've seen, many protists are photoautotrophs and contain chloroplasts. Many others are heterotrophs, absorbing organic molecules or ingesting larger food particles; such heterotrophic protists include important mutualistic and parasitic species. Still other protists are mixotrophs that combine photosynthesis *and* heterotrophic nutrition. Photoautotrophy, heterotrophy, and mixotrophy have all arisen independently in many different protist lineages. In part as a result of this nutritional and taxonomic diversity, protist producers and symbionts are abundant in natural communities and have large ecological effects.

Photosynthetic Protists

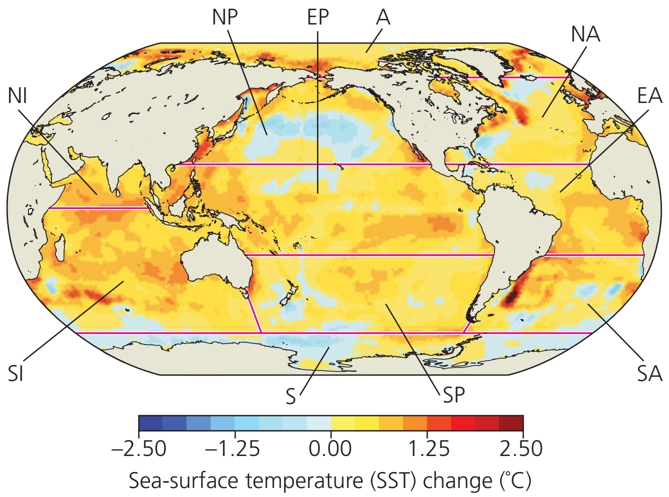
Many protists are important **producers**, organisms that use energy from light (or inorganic chemicals) to convert carbon dioxide to organic compounds. Producers form the base of ecological food webs. In aquatic communities, the main producers are photosynthetic protists and prokaryotes. All other organisms in the community depend on them for food, either directly (by eating them) or indirectly (by eating an organism that ate a producer; **Figure 25.23**). 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 land plants are responsible for the remaining 50%.



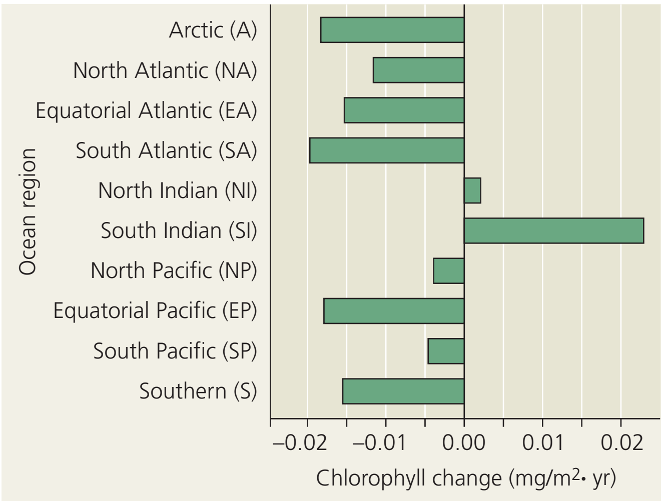
▲ **Figure 25.23 Protists: key producers in aquatic communities.** Arrows in this simplified food web lead from food sources to the organisms that eat them.

Because producers form the foundation of food webs, factors that affect producers can 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, some of the fertilizer applied to a field may be washed by rain 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. For example, earlier in the chapter we mentioned that diatoms can affect global carbon dioxide levels. This effect can result from a chain of events that occurs when ample nutrients produce a rapid increase (a bloom) in diatom abundance. 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. Diatoms that sink to the ocean floor are not very likely to be broken down by bacteria and other decomposers. Hence, the carbon in their bodies remains there, rather than being released as carbon dioxide as the decomposers respire. The overall effect of these events is that carbon dioxide absorbed by diatoms during photosynthesis is transported, or "pumped," to the ocean floor. With an eye toward reducing global warming by lowering atmospheric carbon dioxide levels, some scientists advocate promoting diatom blooms by fertilizing the ocean with essential nutrients such as iron. Other scientists question this strategy, noting that small-scale tests of this idea have yielded mixed results and that it is difficult to predict the effects of large-scale manipulations of ecological communities.



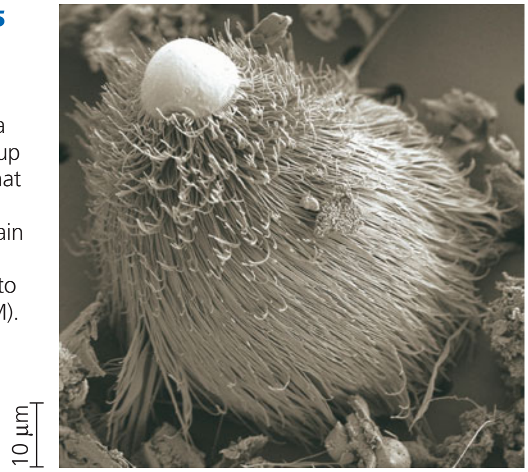
(a) Researchers studied 10 ocean regions, identified with letters on the map (see (b) for the corresponding names). SSTs have increased since 1950 in most areas of these regions.



(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.

▲ **Figure 25.24 Effects of climate change on marine producers.**

A related and pressing question is how global warming will affect photosynthetic protists and other producers. Satellite data and historical observations show that the growth of photosynthetic protists and prokaryotes has declined in many ocean regions as sea surface temperatures have increased **(Figure 25.24)**. 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, these changes would likely have far-reaching effects on marine ecosystems, fishery yields, and the global carbon cycle (see Chapter 42).



▶ **Figure 25.25 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).

Symbiotic Protists

Many protists form symbiotic associations with other species. For example, photosynthetic dinoflagellates are food-providing symbiotic partners of the coral polyps that build coral reefs. Coral reefs are highly diverse ecological communities. That diversity ultimately depends on corals—and on the mutualistic protist symbionts 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 25.25)**. 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 feed on the tissues of plants or animals. Among the species that parasitize plants, the stramenopile *Phytophthora ramorum* 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 California and Oregon (see Chapter 41). A closely related species, *P. infestans*, causes potato late blight, which turns the stalk and stem of potato plants to 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, destroying as much as 70% of the crop in some areas.

We'll close the chapter by taking a closer look at the parasitic protists that cause disease in humans.

Effects on Human Health

Our bodies are home to many symbiotic species, including some protists that can cause disease. While bacteria and viruses may be the pathogens that most readily come to mind, protists that cause infectious disease can pose major challenges, both to our immune systems and to public health.

Consider *Trypanosoma*, the excavate that causes sleeping sickness (see Figure 25.12). This disease is fatal if not treated.

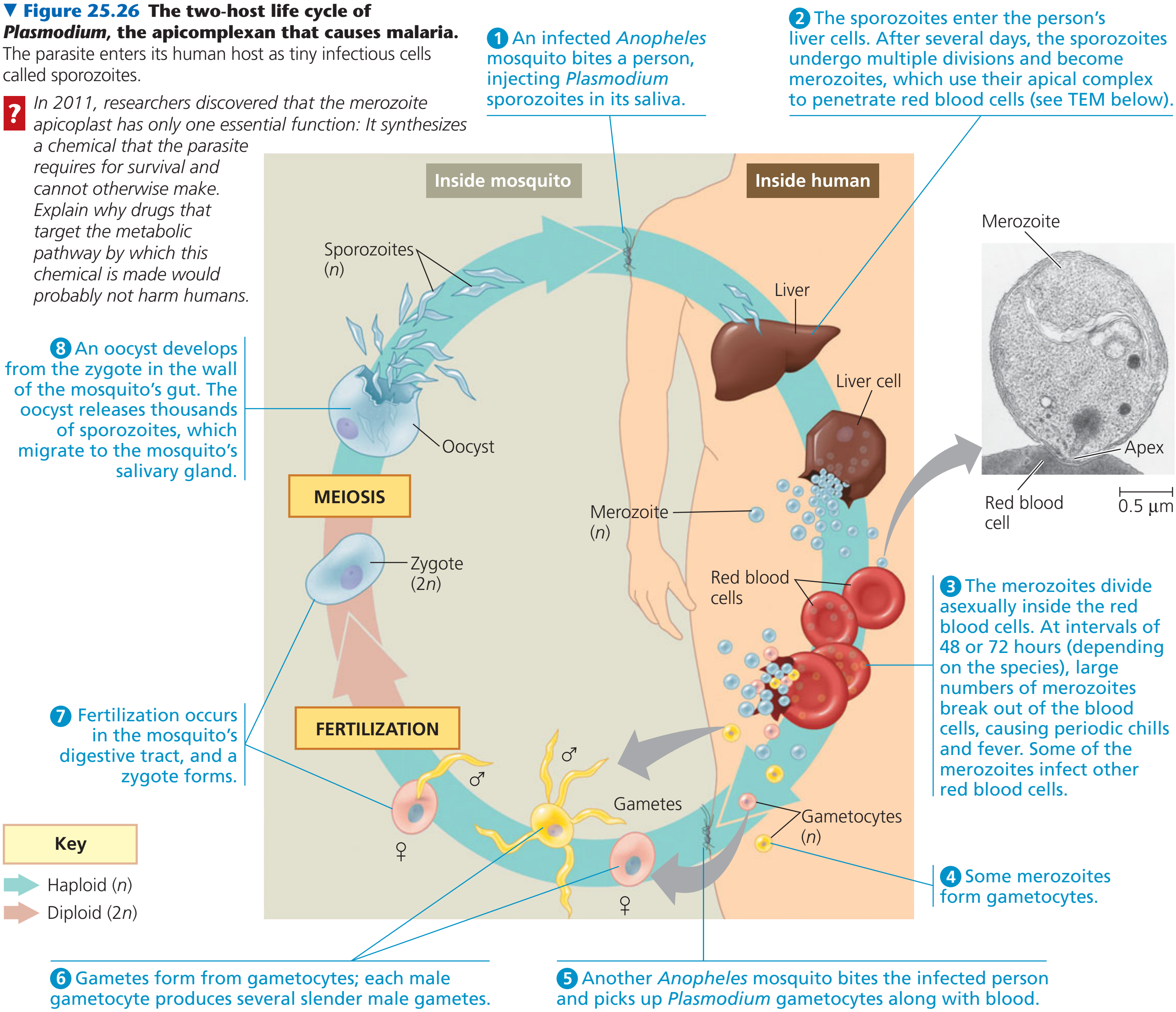
Trypanosomes evade immune responses with an effective "bait-and-switch" defense. The surface of a trypanosome is coated with millions of copies of a single protein. However, before the host's immune system can recognize the protein and mount an attack, new generations of the parasite switch to another surface protein with a different molecular structure. Frequent changes in the surface protein prevent the host from developing immunity. About a third of *Trypanosoma*'s genome is dedicated to producing these surface proteins.

A group of alveolates, the **apicomplexans**, includes protists that cause serious human diseases such as malaria. Nearly all apicomplexans are parasites of animals—and virtually all animal species examined so far are attacked by these parasites. Although apicomplexans are not photosynthetic, they retain a modified plastid (*apicoplast*), most likely of red algal origin (see Figure 25.4). Apicomplexans typically 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 25.26)**.

Historically, malaria has rivaled tuberculosis (which is caused by a bacterium) 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 250 million people in the tropics are currently infected, and 900,000 die each year. Efforts are under way to develop new methods of treatment, including drugs that target the

▼ Figure 25.26 The two-host life cycle of *Plasmodium*, the apicomplexan that causes malaria. The parasite enters its human host as tiny infectious cells called sporozoites.

? *In 2011, researchers discovered that the merozoite apicoplast has only one essential function: It synthesizes a chemical that the parasite requires for survival and cannot otherwise make. Explain why drugs that target the metabolic pathway by which this chemical is made would probably not harm humans.*



apicoplast. This approach may be effective because the apicoplast, derived by secondary endosymbiosis from a prokaryote, has metabolic pathways different from those in humans.

As we've seen in this chapter, the origin of eukaryotes had an enormous impact on the history of life, leading to a great increase in the structural diversity of cells and ultimately to the rise of large, multicellular organisms. These changes set the stage for the events we'll describe in the next two chapters: the colonization of land by plants and fungi (Chapter 26) and the ecological and evolutionary effects resulting from the origin of animals (Chapter 27).

CONCEPT CHECK 25.4

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. Predict how such "coral bleaching" would affect corals and other species in the community.

For suggested answers, see Appendix A.

25 Chapter Review

SUMMARY OF KEY CONCEPTS

CONCEPT 25.1

Eukaryotes arose by endosymbiosis more than 1.8 billion years ago (pp. 481–487)

- Domain Eukarya contains many groups of **protists**, along with plants, animals, and fungi. Eukaryotic cells have a nucleus and other membrane-enclosed organelles, unlike the cells of prokaryotes. These membrane-enclosed organelles make the cells of eukaryotes more complex than the cells of prokaryotes. Eukaryotic cells also have a well-developed cytoskeleton that enables them to have asymmetric forms and to change in shape as they move, feed, or grow.
- The oldest fossils of eukaryotes are of single-celled organisms that lived 1.8 billion years ago. By 1.5 billion years ago, some fossil eukaryotes had asymmetric forms, indicating a well-developed cytoskeleton. Other biological innovations, such as complex multicellularity and sexual life cycles, were in place by 1.2 billion years ago. Larger eukaryotes appeared in the fossil record about 600 million years ago.
- DNA sequence analyses indicate that eukaryotes contain a mixture of archaeal and bacterial genes and cellular characteristics. According to **endosymbiont theory,** this mixture of features likely resulted because eukaryotes originated when an archaeal host (or a host with archaeal ancestors) engulfed a bacterium that would later become an organelle found in all eukaryotes, the mitochondrion.
- In addition to mitochondria, plastids are also thought to be descendants of bacteria that were engulfed by an early eukaryote and became endosymbionts. The plastid-bearing lineage eventually evolved into **red algae** and **green algae**. Other groups of photosynthetic protists evolved from secondary endosymbiosis events in which red algae or green algae were themselves engulfed.

? *What evidence indicates that mitochondria arose before plastids in eukaryotic evolution?*

CONCEPT 25.2

Multicellularity has originated several times in eukaryotes (pp. 487–489)

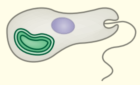
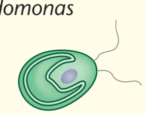
- The first multicellular eukaryotes were colonies, collections of cells that are connected to one another but show little or no cellular differentiation.
- Complex multicellular eukaryotes—those with differentiated cell types—arose independently in a variety of eukaryotic groups, including plants, fungi, animals, and several lineages of algae.
- Genomic analyses suggest that a transition to multicellularity from unicellular ancestors does not require the origin of large numbers of novel genes; instead, such transitions can result primarily from changes in how existing genes are used.

? *Describe an example that illustrates the role of co-opting genes in the origin of complex multicellular eukaryotes from their unicellular ancestors.*

CONCEPT 25.3

Four "supergroups" of eukaryotes have been proposed based on morphological and molecular data (pp. 489–498)

- In one hypothesis, eukaryotes are grouped into four supergroups, each a monophyletic clade. Each eukaryotic supergroup contains a great diversity of organisms, most of which are unicellular.

Supergroup	Major Clades	Specific Example
Excavata	Diplomonads, parabasalids, euglenozoans	*Euglena* 
"SAR" clade	Stramenopiles, alveolates, rhizarians	*Plasmodium* 
Archaeplastida	Red algae, green algae, land plants	*Chlamydomonas* 
Unikonta	Amoebozoans, opisthokonts	*Amoeba* 

- The root of the eukaryotic tree is not known. An approach based on a tracing the occurrence of a rare evolutionary event suggests that the unikonts were the first eukaryotes to diverge from other eukaryotes. This hypothesis will require more supporting evidence before it is widely accepted.

? *Summarize recent changes in our understanding of the evolutionary history of eukaryotes, beginning with an explanation for why kingdom Protista has been abandoned.*

CONCEPT 25.4

Single-celled eukaryotes play key roles in ecological communities and affect human health (pp. 499–506)

- The most elaborate of all cells, unicellular protists use subcellular organelles to accomplish the essential biological functions that multicellular organisms perform with organs. Protists live in a wide range of habitats and include many different lineages of photoautotrophic, heterotrophic, and mixotrophic species.
- 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.
- Protists form a wide range of mutualistic and parasitic relationships that affect their symbiotic partners and many other members of the community. Some protists, such as the malaria parasite *Plasmodium*, pose major challenges to human health.

? *Describe several protists that are ecologically important.*

TEST YOUR UNDERSTANDING

Level 1: Knowledge/Comprehension

1. The oldest fossil eukaryote that can be resolved taxonomically is of
   - **a.** a red alga that lived 1.2 billion years ago.
   - **b.** a red alga that lived 635 million years ago.
   - **c.** a fungus that lived 2 billion years ago.
   - **d.** a fungus that lived 550 million years ago.
   - **e.** an Ediacaran that lived 550 million years ago.
2. The evolution of complex multicellularity in eukaryotes
   - **a.** occurred only once, in the common ancestor of all eukaryotes.
   - **b.** occurred only once, in the common ancestor of all multicellular eukaryotes.
   - **c.** occurred only once, in the animal lineage.
   - **d.** is not documented by the fossil record.
   - **e.** occurred independently in several different eukaryotic lineages.
3. 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.
   - **e.** budding of the plastids from the nuclear envelope.
4. 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.
   - **e.** mitochondrial proteins are synthesized on cytosolic ribosomes, whereas plastids utilize their own ribosomes.
5. Which group is *incorrectly* paired with its description?
   - **a.** rhizarians—morphologically diverse group that includes amoebas with threadlike pseudopodia
   - **b.** diatoms—important producers in aquatic communities
   - **c.** red algae—acquired plastids by secondary endosymbiosis
   - **d.** apicomplexans—parasites with intricate life cycles
   - **e.** diplomonads—protists with modified mitochondria

Level 2: Application/Analysis

6. Based on the phylogenetic tree in Figure 25.9, which of the following statements is correct?
   - **a.** The most recent common ancestor of Excavata is older than that of the SAR clade.
   - **b.** The most recent common ancestor of the SAR clade is older than that of Unikonta.
   - **c.** The most recent common ancestor of red algae and land plants is older than that of nucleariids and fungi.
   - **d.** The most basal (first to diverge) eukaryotic supergroup cannot be determined.
   - **e.** Excavata is the most basal eukaryotic supergroup.

Level 3: Synthesis/Evaluation

7. **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 25.26 and Concept 21.3.)
8. **SCIENTIFIC INQUIRY**
   Applying the "If … then" logic of science (see Chapter 1), 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. **FOCUS ON EVOLUTION**
   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, the SAR clade, 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.)
10. **FOCUS ON 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).

For selected answers, see Appendix A.

26

The Colonization of Land by Plants and Fungi

KEY CONCEPTS

26.1 Fossils show that plants colonized land more than 470 million years ago

26.2 Fungi played an essential role in the colonization of land

26.3 Early land plants radiated into a diverse set of lineages

26.4 Seeds and pollen grains are key adaptations for life on land

26.5 Land plants and fungi fundamentally changed chemical cycling and biotic interactions

▼ **Figure 26.1** How have plants and fungi changed the world?

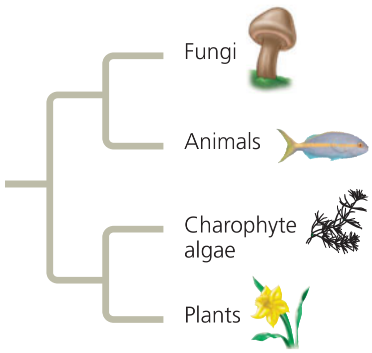
OVERVIEW

The Greening of Earth

Looking at a lush landscape, such as the forest scene in **Figure 26.1**, it is difficult to imagine the terrestrial environment without plants* or other organisms. Yet for more than 2 billion years of Earth's history, the land surface was largely lifeless. Geochemical and fossil evidence suggest that this had changed by 1.2 billion years ago, by which time thin coatings of cyanobacteria and protists existed on land. But it was only within the last 500 million years that fungi as well as small plants and animals joined them ashore. Finally, by about 385 million years ago, some plants appeared that could grow much taller, leading to the formation of the first forests (though with a very different set of species than those in Figure 26.1).

In this chapter, we'll examine the colonization of land by plants and fungi; we'll turn to animals in Chapter 27. Although plants and fungi are not closely related **(Figure 26.2)**, we discuss them together in this chapter in part because fossil evidence suggests that they both arrived on land before animals, which depend on them to survive. Plants supply oxygen and ultimately most of the food eaten by terrestrial animals. Also, plant roots create habitats for animals and other organisms by stabilizing the soil in many terrestrial environments. Fungi break down organic material and recycle nutrients, allowing other organisms to assimilate essential chemical elements.

Fossil evidence also suggests that plants colonized land in partnership with fungi. This partnership and the diversification of plants and fungi that occurred in terrestrial environments fundamentally changed biotic interactions and chemical cycling. We'll begin this story with the origin of plants, an event that occurred over millions of years as the algal ancestors of early plants adapted to life in a new environment—land.



▲ **Figure 26.2 Relationships among multicellular eukaryotes.** As shown in this phylogenetic tree, fungi and animals are more closely related than either group is to plants or charophytes (or other algae).

*Although a few plant species returned to aquatic habitats during their evolution, most present-day plants live on land. In this chapter, we often refer to all plants as *land* plants, even those that are now aquatic, to distinguish them from algae, which are photosynthetic protists.

CONCEPT 26.1

Fossils show that plants colonized land more than 470 million years ago

Evidence in the form of fossils documents key steps in the origin of plants from their algal ancestors. As you read in Chapter 25, researchers have identified green algae called charophytes as the closest living relatives of land plants (see Figure 26.2). After discussing evidence for this relationship, we'll describe the terrestrial adaptations and fossil record of early land plants.

Evidence of Algal Ancestry

Many key traits of land plants also appear 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.

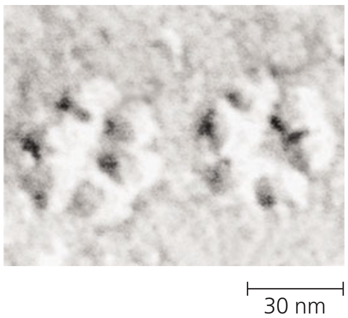
However, the charophytes are the only present-day algae that share certain distinctive traits with land plants, suggesting that they are the closest living relatives of plants. For example, the cells of both land plants and charophytes have distinctive circular rings of proteins in the plasma membrane **(Figure 26.3)**; 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 land plants that have flagellated sperm, the structure of the sperm closely resembles that of charophyte sperm.

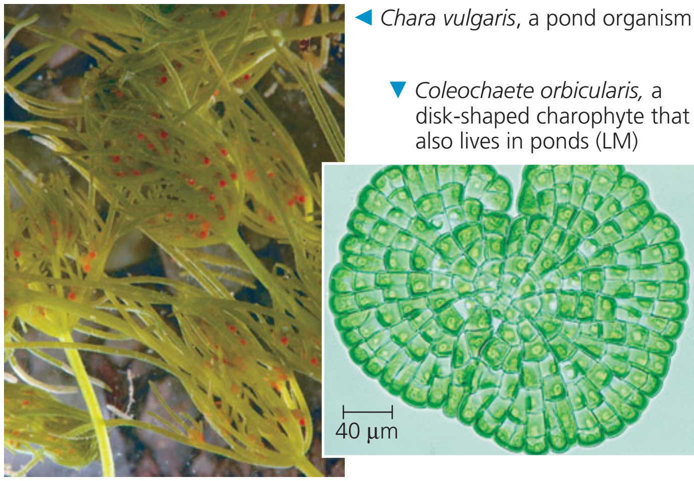
Biochemical studies and analyses of nuclear and chloroplast genes from a wide range of plants and algae also indicate that charophytes—particularly *Chara* and *Coleochaete*—are the closest living relatives of land plants **(Figure 26.4)**. Note that this does not mean that plants are descended from these living algae; however, present-day charophytes may tell us something about what the algal ancestors of plants were like.

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 water. 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 the spores of plants.

▶ **Figure 26.3 Rings of cellulose-synthesizing proteins.** These circular sets of proteins embedded in the plasma membrane are found only in land plants and charophyte algae (SEM).





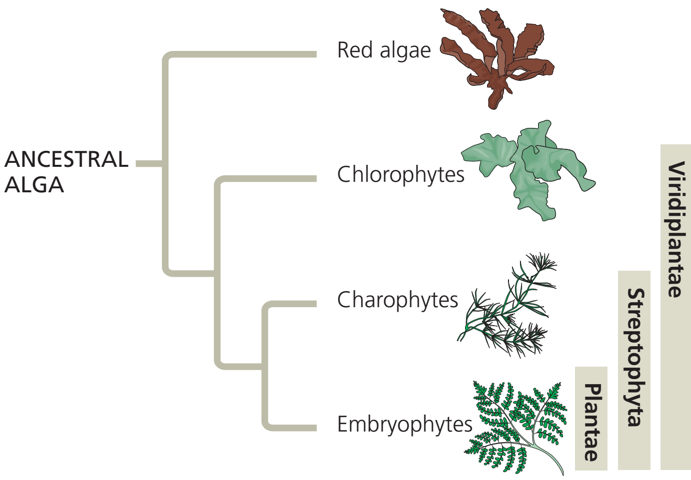
◀ *Chara vulgaris*, a pond organism

▼ *Coleochaete orbicularis*, a disk-shaped charophyte that also lives in ponds (LM)

▲ **Figure 26.4 Examples of charophytes, the closest algal relatives of land plants.**

The accumulation of such traits by at least one population of charophyte ancestors probably enabled their descendants—the first land 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 sags when taken out of water.) Land plants diversified as adaptations evolved that enabled plants 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 26.5)**. Since the placement of this boundary is the



▲ **Figure 26.5 Three possible "plant" kingdoms.**

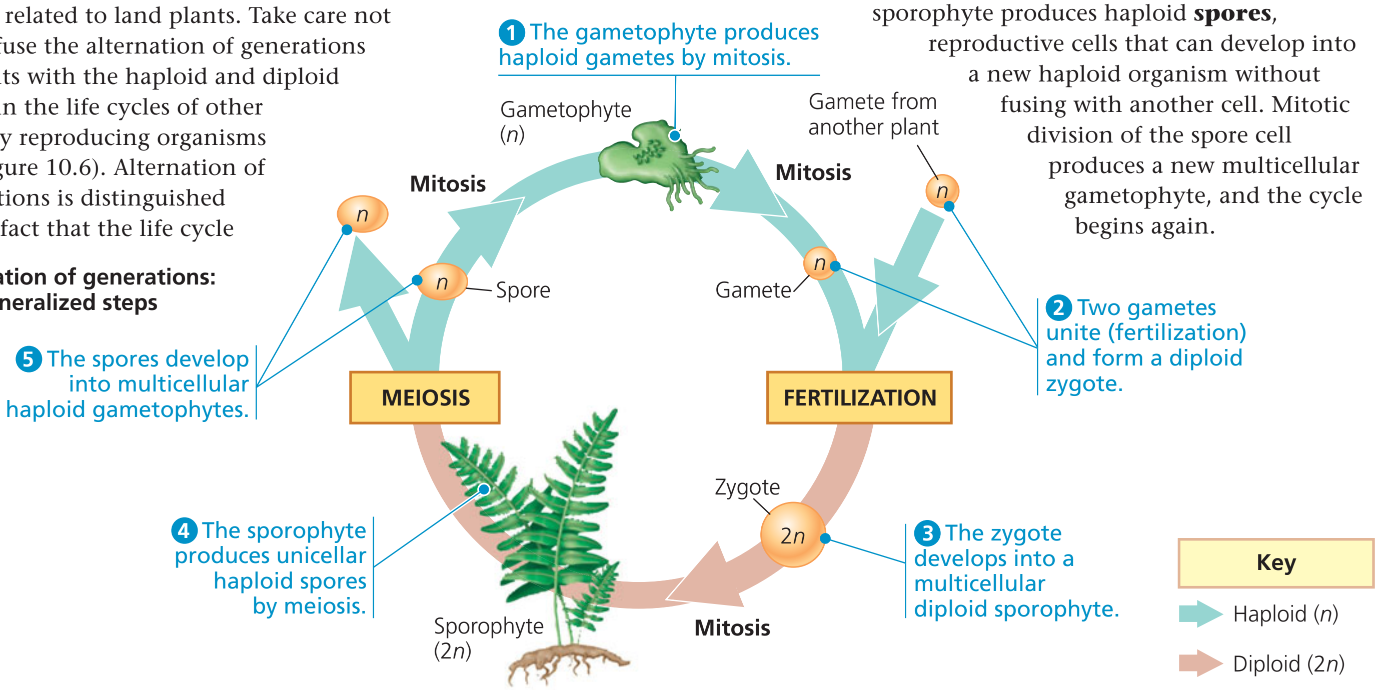
▼ Figure 26.6 Exploring Alternation of Generations

Charophyte algae lack the key traits of land plants described in this figure: alternation of generations and the associated trait of multicellular, dependent embryos. As described on the facing page, 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 land plants and charophytes but instead evolved as derived traits of land plants.

Alternation of Generations

The life cycles of all land 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 land 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 (see Figure 10.6). 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.

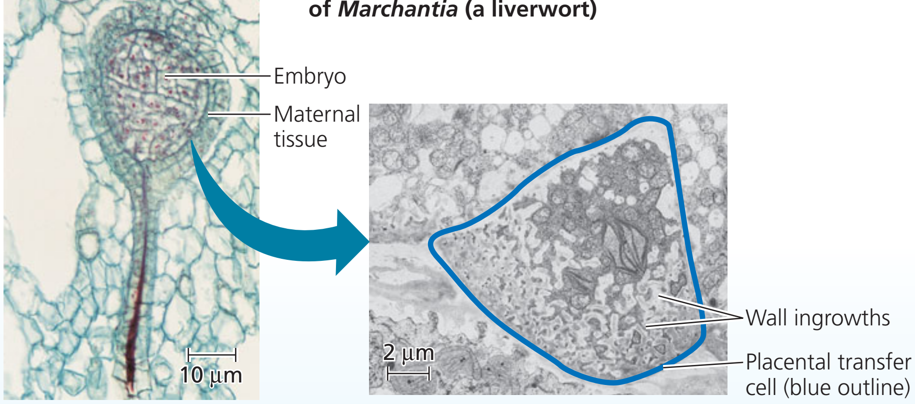
Alternation of generations: five generalized steps



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 land plants is such a significant derived trait that land 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 10.6. Identify which type of sexual life cycle has alternation of generations, and summarize how it differs from other life cycles.*

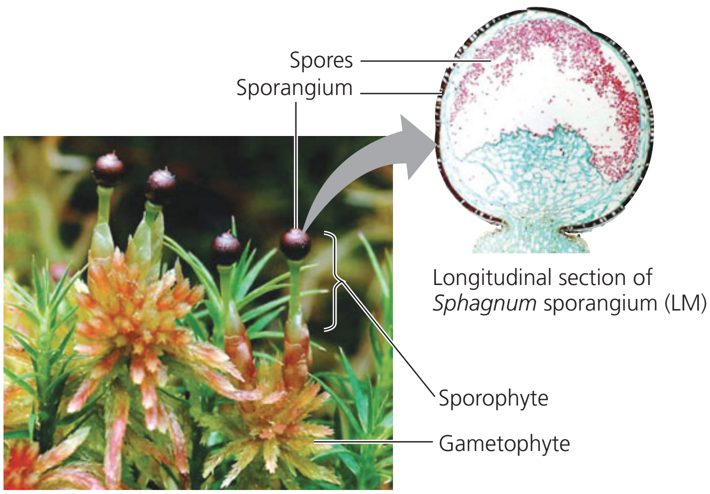
subject of ongoing debate, this text uses a traditional definition that equates the kingdom Plantae with embryophytes (plants with embryos). In this context, let's now examine the derived traits that separate land plants from their closest algal relatives.

Derived Traits of Plants

A series of adaptations that facilitate survival and reproduction on dry land emerged after land plants diverged from their algal relatives. Examples of such traits that are found in land plants but not in the 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 26.6**, on the preceding page.
- **Walled spores produced in sporangia.** The sporophyte stage of the plant life cycle has multicellular organs called **sporangia** (singular, *sporangium*) that produce spores **(Figure 26.7)**. 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.** Land plants also differ from their algal ancestors in having **apical meristems**, localized regions of cell division at the tips of roots and shoots (see Figure 28.16). 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**, that consists of wax and other polymers. Permanently exposed to the air, land plants run a far greater risk of desiccation (drying out) than their algal ancestors. 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 8.3). Stomata are also the main avenues by which water evaporates from the plant; in hot, dry conditions, the stomata close, minimizing water loss. As we describe in the next section, fossil evidence documents the appearance of stomata and other novel traits in early land plants.



▲ **Figure 26.7 Sporophytes and sporangia of a moss (*Sphagnum*).** Each of the many spores produced by a sporangium is encased by a durable, sporopollenin-enriched wall.

Early Land Plants

The algae from which land plants evolved include many unicellular and small, colonial species. Since their ancestors were small, the search for the earliest fossils of land plants has focused on the microscopic world. As mentioned earlier, microorganisms colonized land as early as 1.2 billion years ago. But the microscopic fossils documenting life on land changed dramatically 470 million years ago with the appearance of spores from early land plants.

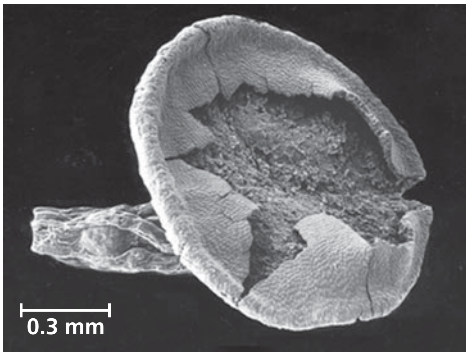
What distinguishes these spores from those of algae or fungi? One clue comes from their chemical composition, which matches that found in plant spores but differs from that in the spores of other organisms. In addition, the structure of the walls of these ancient spores shows features found only in the spores of certain land plants (liverworts). And in rocks dating to 450 million years ago, researchers have discovered similar spores embedded in plant cuticle material that resembles spore-bearing tissue in living plants **(Figure 26.8)**.

It is not surprising that spores provide the earliest fossil evidence of land plants. For one thing, plants produce large numbers of widely dispersed spores. In addition, recall that plant spores contain sporopollenin, a durable compound that allows the spores to be well represented in the fossil record. Larger plant structures, such as the spore-producing structure

(a) Fossilized spores. The chemical composition and physical structure of these 450 million-year-old spores match those found in land plants.

(b) Fossilized sporophyte tissue. The spores in (a) were embedded in tissue that appears to be from plants.

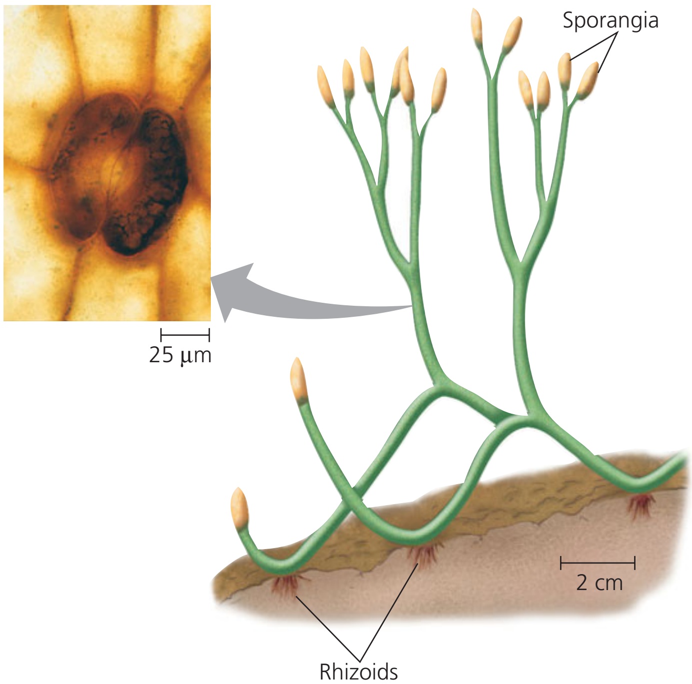
▲ **Figure 26.8 Ancient plant spores and tissue** (colorized SEMs).



▶ ***Cooksonia* sporangium fossil (425 million years old).**

(sporangium) from *Cooksonia* shown above, first appear in the fossil record dating to 425 million years ago. By 400 million years ago, a diverse assemblage of plants lived on land. Some of these early plants had key traits not found in their algal ancestors, including specialized tissues for water transport, stomata, and branched sporophytes **(Figure 26.9)**. Although these early plants were less than 20 cm tall, their branching enabled their bodies to become more complex. As plant bodies became increasingly complex, competition for space and sunlight probably increased. That competition may have stimulated still more evolution in later plant lineages—eventually leading to the formation of the first forests.

Overall, the fossil record shows that by 400 million years ago, early land plants differed greatly from their algal ancestors. As they adapted to life on land, plants evolved a suite of novel features, including sporopollenin-containing spores, cuticles, stomata, transport systems, and branched sporophytes. In addition, early land plants formed a key symbiotic association with the group we turn to next, the fungi.



▲ **Figure 26.9** ***Aglaophyton major*, an early land plant.** This reconstruction from 405-million-year-old fossils exhibits dichotomous (Y-shaped) branching with sporangia at the ends of the branches. *Aglaophyton* had rhizoids that anchored it to the ground. The inset shows a fossilized stoma of *A. major* (colorized LM).

CONCEPT CHECK 26.1

1. Why do researchers identify charophytes rather than another group as the closest relatives of land plants?
2. Identify three derived traits that distinguish plants from charophytes *and* facilitate life on land.
3. Describe fossil evidence of early land plants.
4. **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 26.2

Fungi played an essential role in the colonization of land

The earliest land plants lacked true roots and leaves. Without roots, how did these plants absorb nutrients from the soil? Fossil evidence reveals an adaptation that may have aided their uptake of nutrients: They formed symbiotic associations with fungi. We'll describe these associations, called *mycorrhizae*, a little later in the chapter. For now, the main point is that mycorrhizal fungi form extensive networks of filaments through the soil and transfer nutrients to their symbiotic plant partners. This benefit may have helped plants without roots to colonize land.

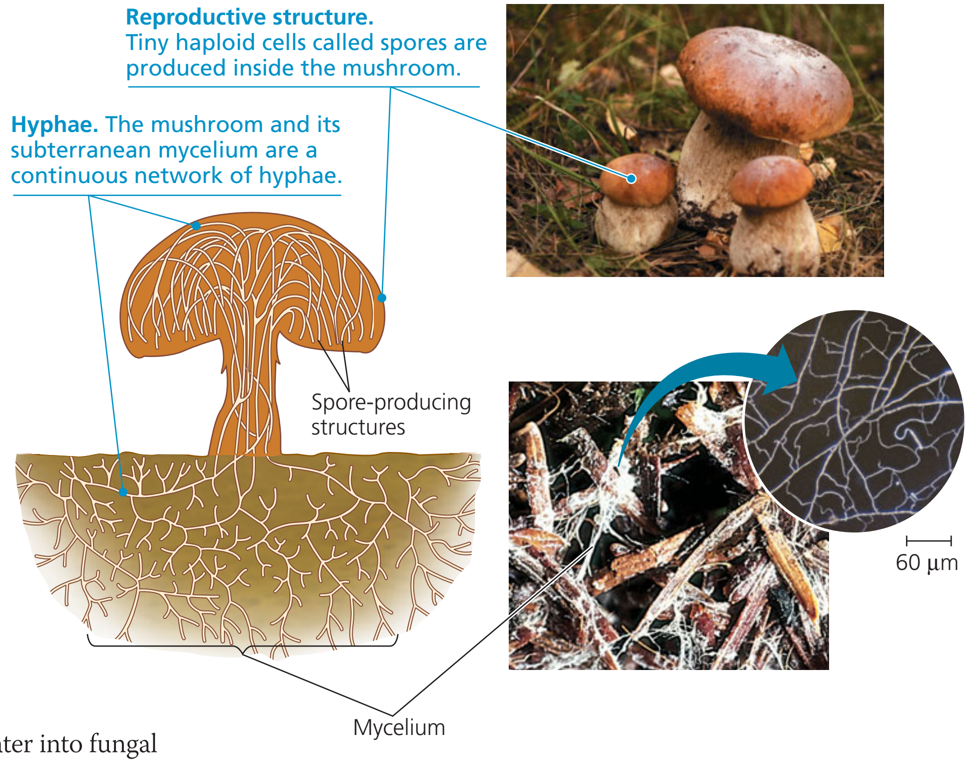
Fungi may, in fact, have colonized land before plants. Once on land, fungi diversified into a wide range of living species. To help us interpret the role fungi played in the colonization of land, we'll begin by examining some of their key features, including how they feed and reproduce.

Fungal Nutrition

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; in brief, fungi are heterotrophs that feed by absorption. Many fungi accomplish this task by secreting hydrolytic enzymes into their surroundings. These enzymes break down complex molecules to smaller organic compounds that the fungi can absorb into their bodies and use. Collectively, fungi can digest compounds from a wide range of sources, living or dead.

Adaptations for Feeding by Absorption

What fungal traits facilitate feeding by absorption? One such trait is a cell wall strengthened by **chitin**, a strong but flexible nitrogen-containing polysaccharide. As fungi absorb nutrients from their environment, the concentration of those nutrients in their cells increases; that, in turn, causes water to move into



▶ **Figure 26.10 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.*

fungal cells by osmosis. The movement of water into fungal cells creates pressure that would cause their cells to burst if they were not surrounded by a rigid cell wall.

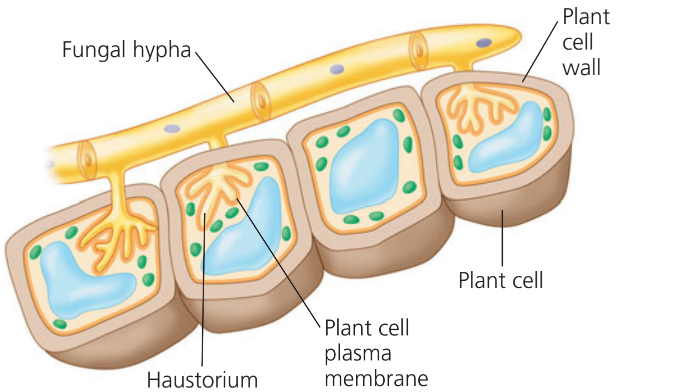
Many fungi also have a structure that increases the efficiency of nutrient absorption. The most common fungal body structures are multicellular filaments and single cells (**yeasts**). Many fungal species can grow as both filaments and yeasts, but even more grow only as filaments; relatively few species grow only as 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 26.10)**. The bodies of these fungi typically form a network of tiny filaments called **hyphae** (singular, *hypha*). Hyphae consist of tubular (chitin-rich) cell walls surrounding the plasma membrane and cytoplasm of the cells. Fungal hyphae form an interwoven mass called a **mycelium** (plural, *mycelia*) that infiltrates the material on which the fungus feeds. 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.

Specialized Hyphae in Mycorrhizal Fungi

Some fungi have specialized hyphae called **haustoria (Figure 26.11)**, which the fungi use to extract nutrients from, or exchange nutrients with, their plant hosts. Mutually beneficial relationships between such fungi and plant roots are called **mycorrhizae** (the term means "fungus roots").

Mycorrhizal fungi (fungi that form mycorrhizae) can improve delivery of phosphate ions and other minerals to plants



▲ **Figure 26.11 Haustoria of mycorrhizae.** Mutualistic mycorrhizal fungi grow specialized hyphae called haustoria that can exchange nutrients with living plant cells. Haustoria remain separated from a plant cell's cytoplasm by the plasma membrane of the plant cell (orange).

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. **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 (see Figure 29.13a). **Arbuscular mycorrhizal fungi** (from the Latin *arbor*, tree) extend branching hyphae through the root cell wall and into tubes formed by invagination (pushing inward) of the root cell plasma membrane (see Figure 29.13b). In the **Scientific Skills Exercise**, you'll interpret data from an experiment studying how mycorrhizae affect plants.

Scientific Skills Exercise

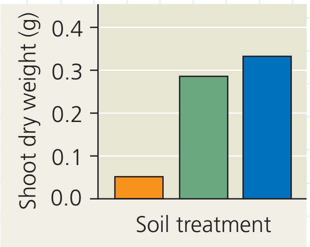
Synthesizing Information from Multiple Data Sets

Can Mycorrhizae Help Plants Cope with High-Temperature Soils? The branching hyphae of arbuscular mycorrhizal (AM) fungi extend through the cell walls of host plants, bringing water and inorganic nutrients into the plant roots in exchange for sugars. Researchers wondered whether AM fungi also can help plants grow in high-temperature (thermal) soils. To study this question, they investigated the role of AM fungi in the growth of *Dichanthelium lanuginosum,* a grass species that grows only in thermal soils.

How the Study Was Done The researchers collected *D. lanuginosum* seeds from geothermally heated soils in Yellowstone National Park. After the seeds germinated, 27 seedlings were transferred to a greenhouse, where they were grown separately in heated pots. Temperatures in the pots ranged from 30°C at the soil surface to 50°C at the base of the pot, comparable to conditions in thermal soils.

Each pot received one of three treatments: nine pots were not inoculated with AM fungi, nine pots were inoculated with nonthermal AM fungi collected from grassland soil in a nongeothermal area, and nine pots were inoculated with thermal AM fungi collected from high-temperature geothermal areas of Yellowstone. All seedlings received the same amount of light and water. After 80 days, all plants were harvested.

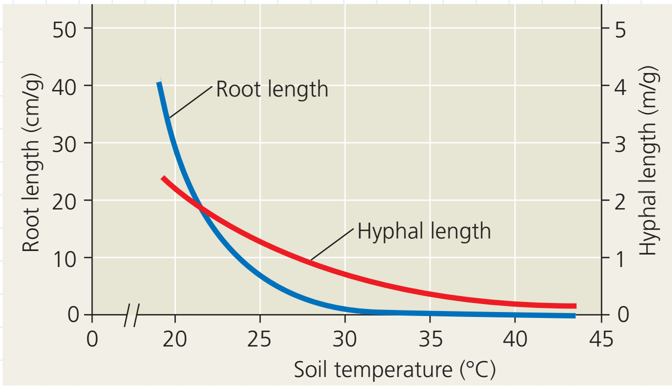
Data from the Study



	Total root length (cm)	Mean root diameter (mm)
No AM fungi	1,800	0.19
Nonthermal AM fungi	4,800	0.23
Thermal AM fungi	4,300	0.22

Interpret the Data

1. Compare the mean dry weight of shoots, total root length, and mean root diameter of *D. lanuginosum* grown in pots with and without inoculation by AM fungi. How do AM fungi appear to affect *D. lanuginosum* plants grown at high temperatures?
2. Compare the mean dry weight of shoots, total root length, and mean root diameter of *D. lanuginosum* in pots inoculated with thermal and nonthermal AM fungi. Do *D. lanuginosum* plants grow equally well when the soil is inoculated with thermal and nonthermal AM fungi? What does this suggest about the thermal tolerances of AM fungi from geothermal and grassland soils?
3. The researchers also measured the length of *D. lanuginosum* roots and the hyphal length of AM fungi in geothermal soils of different temperatures. The curves below, which were estimated from a statistical best fit to the data, show how the average root or hyphal length (per gram of soil) varies with soil temperature. Use these curves to estimate average root and hyphal lengths in soils of 25°C and soils of 35°C.



4. What do the curves in the graph suggest about the relative heat tolerances of *D. lanuginosum* roots and fungal hyphae? How might these results explain the differences in growth of *D. lanuginosum* plants grown in soils with and without AM fungi?

Data from R. Bunn et al., Arbuscular mycorrhizal fungi ameliorate temperature stress in thermophilic plants, *Ecology* 90: 1378–1388 (2009).

MB A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

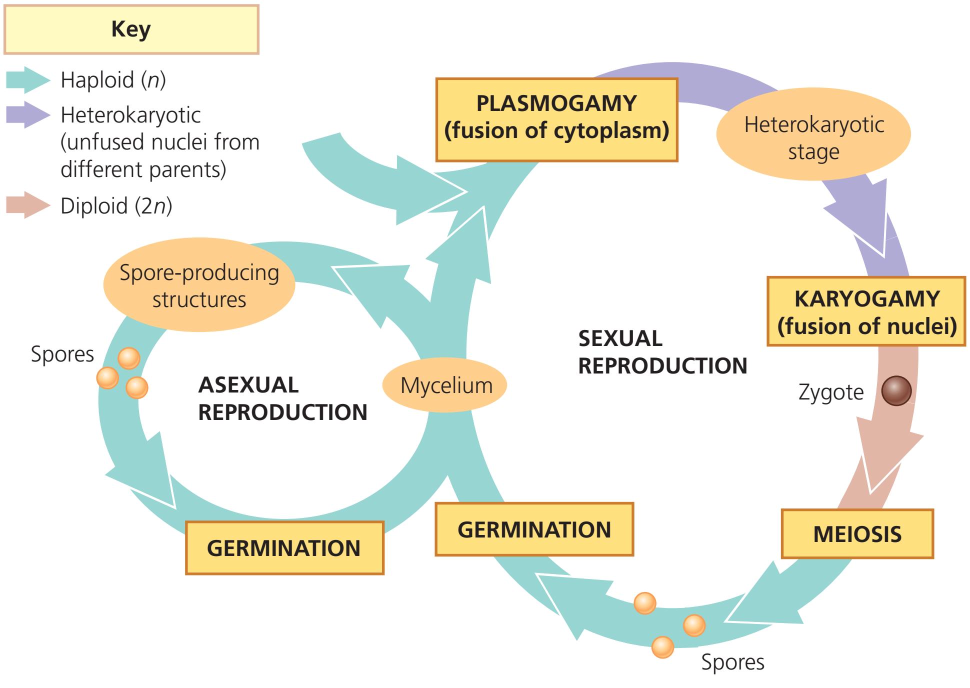
Sexual and Asexual Reproduction

Most fungi propagate themselves by producing vast numbers of spores, either sexually or asexually. Spores can be carried long distances by wind or water. If they land in a moist place where there is food, they germinate, producing new mycelia. **Figure 26.12** generalizes the many different life cycles that can produce fungal spores.

As shown in this figure, the sexual portion of a fungal life cycle typically occurs in two stages. First, the cytoplasms of two parent mycelia fuse, an event known as **plasmogamy**. 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 structures formed during karyogamy are the only diploid stage in most fungi. Meiosis then restores the haploid condition. Many fungi then 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. Other species reproduce asexually as single-celled yeasts that divide to produce genetically identical daughter cells.

The Origin of Fungi

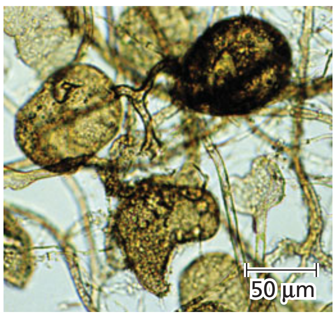
Although fungi were once thought to be closely related to plants, molecular data show that fungi and animals are more closely related to each other than either group is to plants



▲ **Figure 26.12 Generalized life cycle of fungi.** Many—but not all—fungi reproduce both sexually and asexually. Some reproduce only sexually, others only asexually.

or most other eukaryotes (see Figure 25.9). DNA sequence data also indicate that 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. As we discussed in Chapter 25, 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 must have evolved in animals and fungi independently, from different single-celled ancestors.

Based on molecular clock analyses (see Chapter 20), scientists have estimated that the ancestors of animals and fungi diverged into separate lineages 1–1.5 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 most biologists think that fungi originated in aquatic environments, the oldest fossils that are widely accepted as fungi are of terrestrial species that lived about 460 million years ago **(Figure 26.13)**. Overall, additional fossil discoveries will be needed to clarify when fungi originated and what features were present in their earliest lineages.



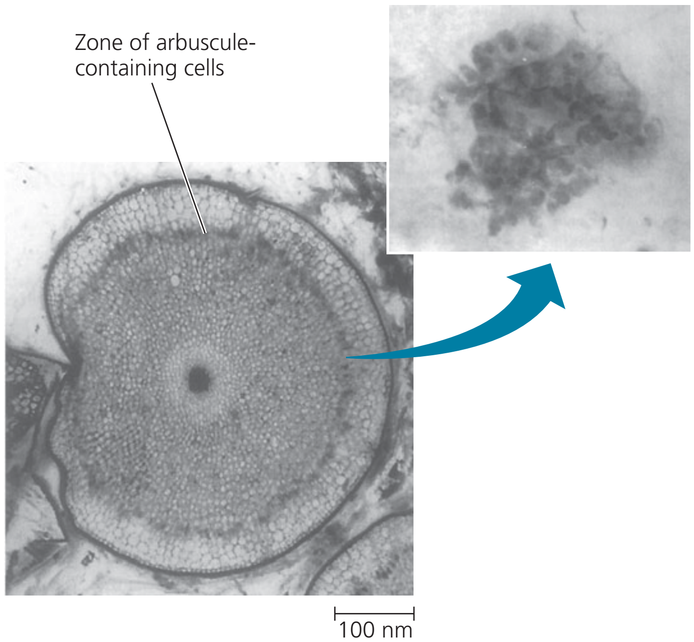
▲ **Figure 26.13 Fossil fungal hyphae and spores from the Ordovician period (about 460 million years ago)** (LM).

The Move to Land

As we mentioned earlier, fungi may 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 rigid cell walls and 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 land plants. For example, 405-million-year-old fossils of the early land plant *Aglaophyton* (see Figure 26.9) contain evidence of mycorrhizal relationships between plants and fungi. This evidence includes fossils of hyphae that have penetrated within plant cells and formed structures that resemble the haustoria of arbuscular mycorrhizae **(Figure 26.14)**. Similar structures have been found in a variety of other early land plants, suggesting that plants probably existed in beneficial relationships with fungi from the earliest periods of colonization of land.

Support for the antiquity of mycorrhizal associations has also come from recent molecular studies. For a mycorrhizal fungus and its plant partner to establish a symbiotic relationship,



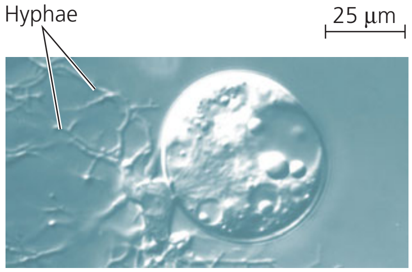
▲ **Figure 26.14 An ancient symbiosis.** This 405-million-year-old fossil stem (cross section) documents arbuscular mycorrhizae in the early land plant *Aglaophyton major.* The inset shows an enlarged view of a cell containing an arbuscule that has branched extensively; the fossil arbuscule resembles those seen today (see Figure 29.13b).

▼ **Figure 26.15** **Exploring Fungal Diversity**

The phylogeny of fungi is currently the subject of much research. Most mycologists recognize five major groups of fungi, although the chytrids and zygomycetes are probably paraphyletic (as indicated by the parallel lines).

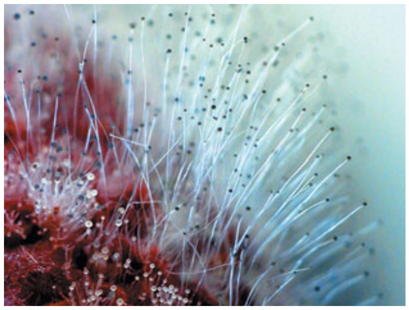
Chytrids (1,000 species)

In chytrids such as *Chytridium*, the globular fruiting body forms multicellular, branched hyphae (LM); other species are single-celled. Ubiquitous in lakes and soil, chytrids have flagellated spores and are thought to include some of the earliest fungal groups to diverge from other fungi.



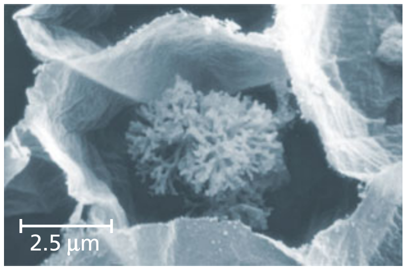
Zygomycetes (1,000 species)

The hyphae of some zygomycetes, including this mold in the genus *Mucor* (LM), grow rapidly in foods such as fruits and bread. As such, the fungi may act as decomposers (if the food is not alive) or parasites; other species live as neutral (commensal) symbionts.



Glomeromycetes (160 species)

The glomeromycetes form arbuscular mycorrhizae with plant roots, supplying minerals and other nutrients to the roots; about 80% of all plant species have such mutualistic partnerships with glomeromycetes. This SEM shows the branched hyphae—an arbuscule—of *Glomus mosseae* bulging into a plant root cell (the root has been treated to remove the cytoplasm).



Ascomycetes (65,000 species)

Also called sac fungi, members of this diverse group are common to many marine, freshwater, and terrestrial habitats. The cup-shaped ascocarp (fruiting body) of the ascomycete shown here (*Aleuria aurantia*) gives this species its common name: orange peel fungus.

Basidiomycetes (30,000 species)

Often important as decomposers and ectomycorrhizal fungi, basidiomycetes, or club fungi, are unusual in having a long-lived, heterokaryotic stage in which each cell has two nuclei (one from each parent). The fruiting bodies—commonly called mushrooms—of this fly agaric (*Amanita muscaria*) are a familiar sight in coniferous forests of the Northern Hemisphere.

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 26.16). 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 the land plant common ancestor—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.

Diversification of Fungi

In the past decade, molecular analyses have helped clarify the evolutionary relationships between fungal groups, although there are still areas of uncertainty. **Figure 26.15** presents a simplified version of one current hypothesis.

The groups shown in Figure 26.15 may represent only a small fraction of the diversity of extant fungi. While there are roughly 100,000 known species of fungi, there may actually be close to 1.5 million species. Two metagenomic studies published in 2011 support such higher estimates: Entirely new groups of unicellular fungi were discovered, and the genetic variation in some of these groups is as large as that across all of the groups in Figure 26.15.

As these phylogenetic data suggest, fungi diversified extensively after they colonized land. So, too, did the land plants that fungi helped ashore, as we'll discuss next.

CONCEPT CHECK 26.2

1. Compare and contrast the nutritional mode of a fungus with your own nutritional mode.
2. Describe the importance of mycorrhizae, both today and in the colonization of land. What evidence supports the antiquity of mycorrhizal associations?
3. **MAKE CONNECTIONS** Review Figures 8.3 and 8.5. 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 mycorrhizal fungus, or in both? Explain.

For suggested answers, see Appendix A.

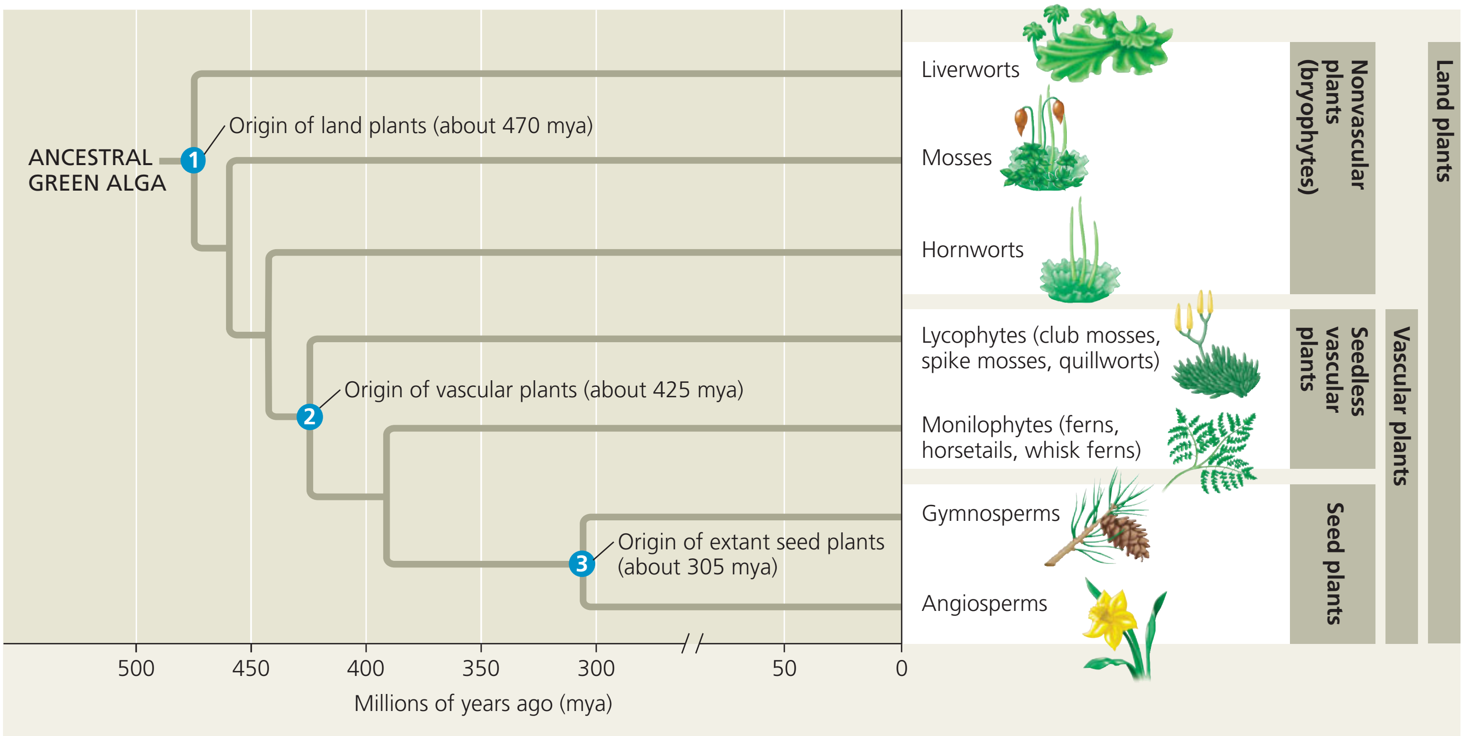
CONCEPT 26.3

Early land plants radiated into a diverse set of lineages

As early land plants adapted to terrestrial environments, they gave rise to the vast diversity of living plants. An overview of that diversity is provided by **Figure 26.16**, which summarizes the evolutionary history of extant plant groups. (Extant lineages are those that have surviving members.)

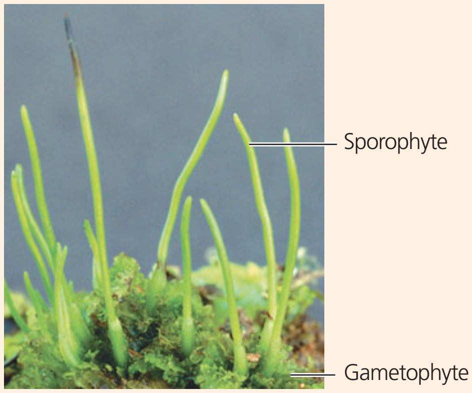
One way to distinguish plant groups is whether they have an extensive system of **vascular tissue**, cells joined into tubes that transport water and nutrients throughout the plant body. Most present-day plants have a complex vascular tissue system and are therefore called **vascular plants**. We'll return to

▼ **Figure 26.16 Highlights of plant evolution.** The phylogeny shown here illustrates a leading hypothesis about the relationships between plant groups.



(a) ***Plagiochila deltoidea*****, a liverwort.** This group's name refers to the shape of its gametophytes. In medieval times, their shape was thought to be a sign that the plants could help treat liver diseases.

(b) ***Polytrichum commune*****, a moss.** Moss gametophytes are less than 15 cm tall in most species but can reach up to 2 m. The familiar carpet of moss you observe consists mainly of gametophytes.



(c) ***Anthoceros*** **sp., a hornwort.** This group's name refers to the long, tapered shape of the sporophyte, which can grow to about 5 cm high.

▲ **Figure 26.17 Bryophytes (nonvascular plants).** Molecular and morphological data indicate that bryophytes are paraphyletic; they do not form a single clade.

vascular plants later in this section, but first we'll discuss the nonvascular plants, or **bryophytes** (from the Greek *bryon*, moss, and *phyton*, plant), an informal name for plants that lack an extensive transport system.

Bryophytes: A Collection of Early-Diverging Plant Lineages

Nonvascular plants (bryophytes)
Seedless vascular plants
Gymnosperms
Angiosperms

The nonvascular plants (bryophytes) are represented today by three clades of small herbaceous (nonwoody) plants: *liverworts*, *mosses*, and *hornworts* **(Figure 26.17)**. Researchers think that these three clades were the earliest lineages to have diverged from the common ancestor of land plants (see Figure 26.16). Fossil evidence provides some support for this idea: The earliest spores of land plants (dating to 470–450 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.

As in some early land plants, the bryophytes of today are anchored to the ground by **rhizoids**, which lack specialized conducting cells and do not play a primary role in water and mineral absorption. Living bryophytes are typically found in moist habitats—as you might expect, since they have flagellated sperm that must swim through a film of water to fertilize an egg. Unlike most plants today, in bryophytes the haploid gametophytes are the dominant stage of the life cycle: The gametophytes are usually larger and longer-living than the sporophytes (see Figure 26.17). The gametophytes of mosses and other bryophytes typically 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. These constraints were removed in the group we turn to next, the vascular plants.

Seedless Vascular Plants: The First Plants to Grow Tall

Nonvascular plants (bryophytes)
Seedless vascular plants
Gymnosperms
Angiosperms

During the first 100 million years of plant evolution, bryophytes were prominent members of the vegetation. But it is vascular plants that dominate most landscapes today. The earliest fossils of vascular plants date to 425–420 million years ago. These plants lacked seeds but had well-developed vascular systems, an evolutionary novelty that set the stage for plants to grow tall.

The rise of vascular plants was accompanied by other evolutionary changes as well, resulting in life cycles with dominant sporophytes and the origin of well-developed roots and leaves. Our focus here will be on the two clades of vascular plants shown in **Figure 26.18**, the **lycophytes** (club mosses and their relatives) and the **monilophytes** (ferns and their relatives). The plants in these clades lack seeds, which is why collectively the two clades are often called **seedless vascular plants**. We'll discuss vascular plants that have seeds in Concept 26.4.

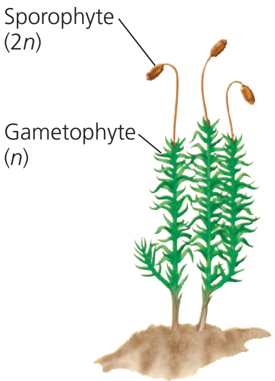
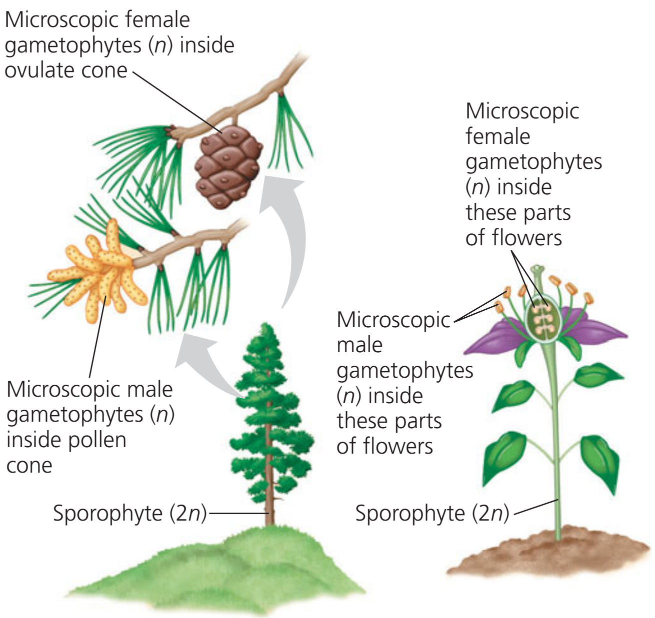
Life Cycles with Dominant Sporophytes

As mentioned earlier, mosses and other bryophytes have life cycles dominated by gametophytes. Fossils suggest that a change began to occur in the ancestors of 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 plant form in the alternation of generations **(Figure 26.19)**. In ferns, for example, the familiar leafy plants are

▶ **Figure 26.18 Lycophytes and monilophytes (seedless vascular plants).** Although lycophytes and monilophytes each form a monophyletic group, seedless vascular plants are paraphyletic.

(a) ***Diphasiastrum tristachyum*, a lycophyte.** The spores of lycophytes such as this club moss are released in clouds and are so rich in oil that magicians and photographers once ignited them to create smoke or flashes of light.

(b) ***Athyrium filix-femina*, a monilophyte.** The sporophytes of ferns typically have horizontal stems that give rise to large leaves called fronds, which grow as their coiled tips unfurl.

	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			

▲ **Figure 26.19 Gametophyte-sporophyte relationships in different plant groups.**

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. However, as in nonvascular plants, the sperm of ferns and all other seedless vascular plants are flagellated and must swim through a film of water to reach eggs.

Transport in Xylem and Phloem

Vascular plants have two types of vascular tissue: xylem and phloem. **Xylem** conducts most of the water and minerals. The xylem of most vascular plants includes **tracheids**, tube-shaped cells that carry water and minerals up from the roots (see Figure 28.9). The water-conducting cells in vascular plants 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 (see Figure 28.9).

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 rapidly. Overall, the ability to grow tall gave vascular plants a competitive edge over nonvascular plants, which rarely grow above 20 cm in height. Competition among vascular plants also increased, and taller growth forms were favored by natural selection—such as the trees that formed the first forests about 385 million years ago.

Evolution of Roots and Leaves

Vascular tissue also provides benefits below ground. In contrast to the rhizoids of bryophytes, roots with vascular tissue 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.

Leaves increase the surface area of the plant body and serve as the primary photosynthetic organ of vascular plants. In terms of size and complexity, leaves can be classified as either microphylls or megaphylls. All of the lycophytes (the oldest lineage of extant vascular plants)—and only the lycophytes—have **microphylls**, small, usually 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 and support greater photosynthetic productivity than microphylls. Microphylls first appear in the fossil record 410 million years ago, but megaphylls do not emerge until about 370 million years ago.

Seedless vascular plants were abundant in the swampy forests and other moist ecosystems of the Carboniferous period (359–299 million years ago). Growing along with these seedless plants were early seed plants. Though seed plants were not dominant at that time, they rose to prominence after the climate became drier at the end of the Carboniferous period. In Concept 26.4, we'll trace the origin and diversification of seed plants, continuing the story of adaptation to life on land.

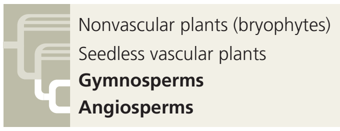
CONCEPT CHECK 26.3

1. How do the main similarities and differences between seedless vascular plants and nonvascular plants influence function in these plants?
2. **MAKE CONNECTIONS** Figure 26.16 identifies lineages as land plants, nonvascular plants, vascular plants, seedless vascular plants, and seed plants. Which of these categories are monophyletic, and which are paraphyletic (see Figure 20.10)? Explain.
3. **MAKE CONNECTIONS** Monilophytes and seed plants both have megaphylls, as well as other traits not found in lycophytes. Explain this observation using Figure 26.16 and the concept of descent with modification (see Concept 19.2).

For suggested answers, see Appendix A.

CONCEPT 26.4

Seeds and pollen grains are key adaptations for life on land

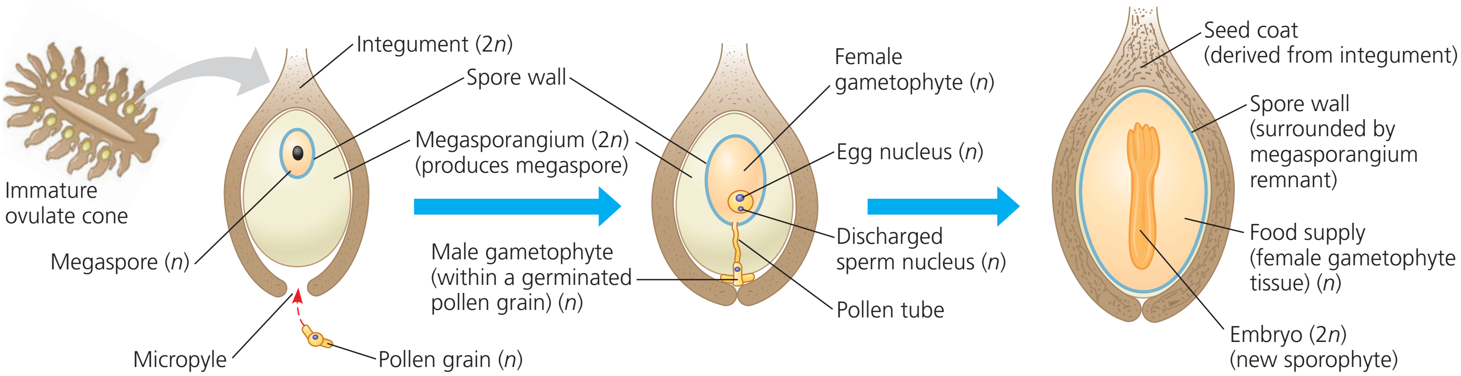


Seed plants originated about 360 million years ago. As this new group of plants became established, they expanded into a broad range of terrestrial environments, dramatically altering the course of plant evolution. This large impact was due in part to the innovation for which this group of plants is named: the seed. 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.

Extant seed plants can be divided into two major clades, gymnosperms (pines and their relatives) and angiosperms (flowering plants). **Gymnosperms** (from the Greek *gymnos*, naked, and *sperm*, seed) are grouped together as "naked seed" plants because their seeds are not enclosed in chambers. In contrast, the seeds of **angiosperms** (from the Greek *angion*, container) develop inside chambers called ovaries. We'll begin our discussion of seed plants with an overview of their adaptations for life on land. Then we'll turn to their origin and evolutionary history.

Terrestrial Adaptations in Seed Plants

In addition to seeds, all seed plants have reduced gametophytes, ovules, and pollen. These adaptations provided new ways for seed plants to cope with terrestrial conditions such as drought and exposure to the ultraviolet (UV) radiation in sunlight. These adaptations also freed seed plants from requiring water for fertilization, enabling reproduction to occur under a broader range of conditions than in seedless plants.



(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.

▲ **Figure 26.20 From ovule to seed in a gymnosperm.**

? *A gymnosperm seed contains cells from how many different plant generations? Identify the cells and whether each is haploid or diploid.*

Reduced Gametophytes

Unlike mosses and other bryophytes, 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. While the gametophytes of seedless vascular plants are visible to the naked eye, the gametophytes of most seed plants are microscopic (see Figure 26.19).

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. The moist reproductive tissues of the sporophyte shield the gametophytes from UV radiation and protect them from drying out. This relationship also enables the dependent gametophytes to obtain nutrients from the sporophyte. In contrast, the free-living gametophytes of seedless vascular plants must fend for themselves.

Ovules and Pollen

Seed plants are unique in retaining the structures that develop into a female gametophyte within the parent sporophyte. Early in this process, a layer of sporophyte tissue called **integument** envelops and protects the tissues that will eventually give rise to the female gametophyte. The integument and the tissues it encloses together make up an **ovule** (**Figure 26.20a**). Inside each ovule, an egg-producing female gametophyte develops from a haploid spore. Spores that produce female gametophytes are called *megaspores* because they are larger than spores that produce male gametophytes (*microspores*).

A microspore develops into a **pollen grain** that consists of a male gametophyte enclosed within the pollen wall. The pollen wall, which contains sporopollenin, protects the gametophyte as it is transported from the parent plant by wind or by hitchhiking on the body of 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 26.20b**.

Recall that 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 are found in moist habitats. But in seed plants, a sperm-producing male gametophyte inside a pollen grain can be carried long distances 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 successful colonization of dry habitats.

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 26.20c**, the whole ovule develops into a seed: the embryo, along with a food supply, packaged within a protective coat derived from the integument.

Until the advent of seeds, the spore was the only protective stage in any plant life cycle. 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. Under favorable conditions, 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.

Early Seed Plants and the Rise of Gymnosperms

Recall from Figure 26.16 that extant seed plants form two sister clades: gymnosperms and angiosperms. How did these two groups arise?

Fossils reveal that by the late Devonian period (about 380 million years ago), some plants had acquired features found in seed plants, such as the megaspores and microspores mentioned earlier. But these plants did not bear seeds and hence are not classified as seed plants. The first seed plants to appear in the fossil record date from around 360 million years ago, 55 million years before the first fossils of extant gymnosperms and more than 200 million years before the first angiosperm fossils. These early seed plants became extinct, and it remains uncertain which of these extinct lineages ultimately gave rise to the gymnosperms.

The earliest fossils of extant gymnosperms are about 305 million years old. These early gymnosperms lived in moist Carboniferous ecosystems still dominated by lycophytes, ferns, and other seedless vascular plants. As the Carboniferous period gave way to the Permian (299 million years ago), the climate became much drier. As a result, the lycophytes and ferns that dominated moist Carboniferous swamps were largely replaced by gymnosperms, which were better suited to the drier climate.

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. Today, gymnosperms remain an important part of Earth's flora **(Figure 26.21)**. For example, vast regions in northern latitudes are covered by forests of cone-bearing gymnosperms called **conifers**, which include spruce, pine, fir, and redwood. Yet despite the ongoing importance of gymnosperms, most terrestrial ecosystems are now dominated by the group we turn to next, the angiosperms.

The Origin and Diversification of Angiosperms

Commonly known as flowering plants, angiosperms are seed plants that produce the reproductive structures called flowers and fruits. Today, angiosperms are the most diverse and widespread of all plants, with more than 250,000 species (about 90% of all plant species). Before considering the evolution of angiosperms, we'll examine their two key adaptations—flowers and fruits.

Flowers and Fruits

The **flower** is a unique angiosperm structure 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 gymnosperms.

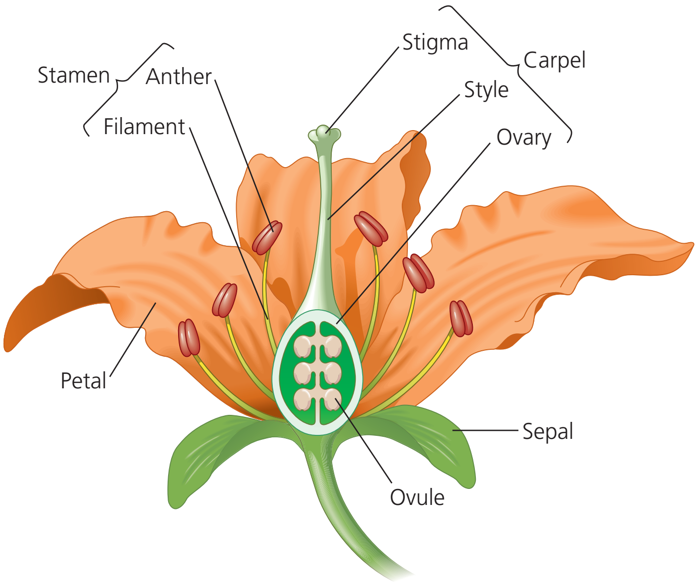
(a) Sago palm (*Cycas revoluta*). This "palm" is actually a cycad, the next largest group of gymnosperms after the conifers (true palms are flowering plants). Cycads have large cones and palmlike leaves.

(b) Douglas fir (*Pseudotsuga menziesii*). This conifer dominates large forested regions and provides more timber than any other North American tree species.

(c) Creeping juniper (*Juniperus horizontalis*). The "berries" of this low-growing conifer are actually ovule-producing cones consisting of fleshy sporophylls.

▲ **Figure 26.21 Examples of gymnosperms.**

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 26.22)**. 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 aid



▲ **Figure 26.22 The structure of an idealized flower.**

in attracting pollinators. Flowers that are wind-pollinated, however, 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. Within the petals are two whorls of fertile floral organs, the stamens and carpels. **Stamens** produce 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** make ovules, which, as in gymnosperms, contain female gametophytes. 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. If fertilized, an ovule develops into a seed.

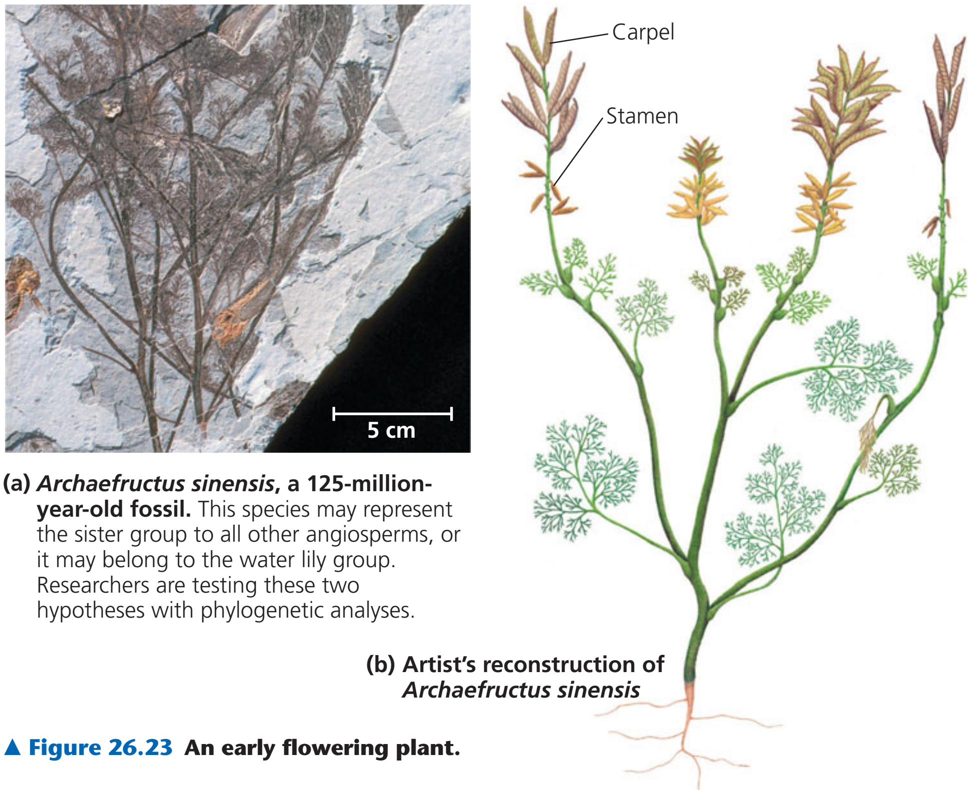
As seeds develop from ovules after fertilization, the ovary wall thickens and the ovary matures into a **fruit**. A pea pod is an example of a fruit, with seeds (mature ovules, the peas) encased in the ripened ovary (the pod). Fruits protect seeds and aid in their dispersal (see Figure 30.12). For example, 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. Many other angiosperms rely on animals to carry seeds. Some of these plants have fruits modified as burrs that cling to animal fur (or the clothes of humans). Other angiosperms 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.

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. 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 Evidence Angiosperms are 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 65 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 (200–145 million years ago), none of these pollen fossils have features diagnostic of angiosperms, suggesting that angiosperms may have originated after the Jurassic. Indeed, the earliest fossils with distinctive angiosperm features are 130-million-year-old pollen grains discovered in China, Israel, and England. Early fossils of larger flowering plant structures include those of *Archaefructus* **(Figure 26.23)** and



(a) *Archaefructus sinensis*, a 125-million-year-old fossil. This species may represent the sister group to all other angiosperms, or it may belong to the water lily group. Researchers are testing these two hypotheses with phylogenetic analyses.

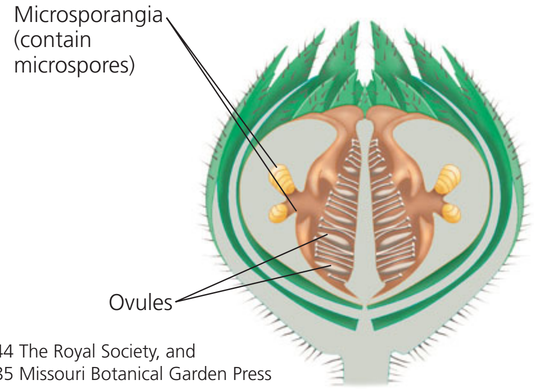
(b) Artist's reconstruction of *Archaefructus sinensis*

▲ **Figure 26.23 An early flowering plant.**

Leefructus, both of which were discovered in China in rocks that are about 125 million years old. 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 common ancestor of angiosperms 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. As we'll see, this conclusion has been supported by recent phylogenetic analyses.

Angiosperm Phylogeny Molecular and morphological evidence suggests that living gymnosperm lineages diverged from the ancestors of angiosperms about 305 million years ago. Indeed, extant angiosperms may be more closely related to several extinct lineages of woody seed plants than they are to living gymnosperms. One such lineage is the Bennettitales, a group with flowerlike structures that may have been pollinated by insects **(Figure 26.24)**.



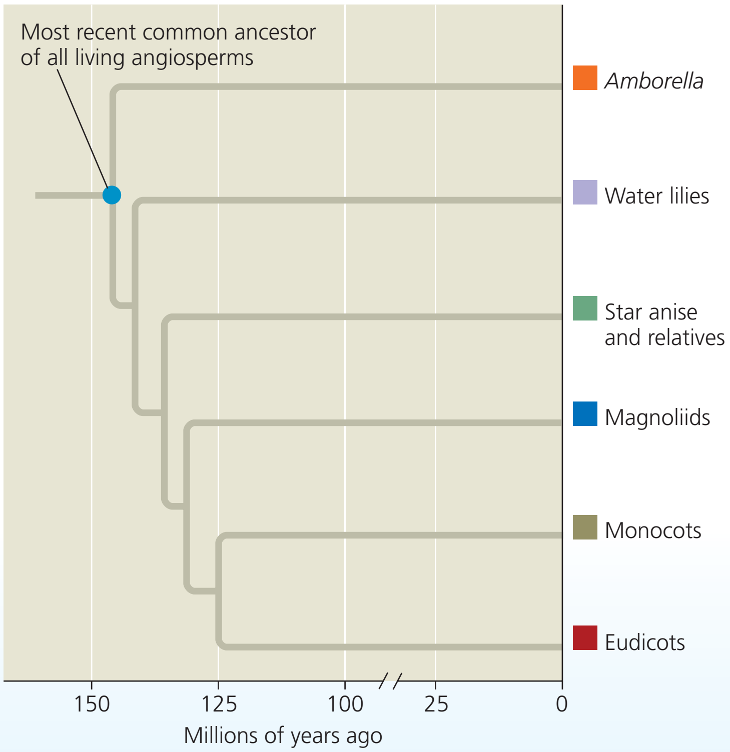
▲ **Figure 26.24 A close relative of the angiosperms?** This reconstruction shows a longitudinal section through the flowerlike structures found in Bennettitales, an extinct group of seed plants hypothesized to be more closely related to extant angiosperms than to living gymnosperms.

MAKE CONNECTIONS *Suppose the Bennettitales and extant angiosperms are sister taxa. Draw a phylogenetic tree that includes Bennettitales, angiosperms, gymnosperms, monilophytes, extant lycophytes. Identify the common ancestor and circle the basal taxon (see Figure 20.5).*

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

▼ Figure 26.25 Exploring Angiosperm Phylogeny

The phylogenetic tree below represents one current hypothesis of angiosperm evolutionary relationships, based on morphological and molecular evidence.



Amborella. This small shrub (*Amborella trichopoda*), 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. *Amborella* lacks vessels, efficient water-conducting cells found in angiosperms in later-diverging lineages.

Water lilies. Species of water lilies (genus *Nymphaea*) are found in aquatic habitats throughout the world. Water lilies are living members of a clade that may be predated only by the *Amborella* lineage.

recent years. Molecular and morphological evidence suggests that a small South Pacific shrub called *Amborella trichopoda* and water lilies are living representatives of two of the most ancient angiosperm lineages **(Figure 26.25)**. *Amborella* is woody, supporting the conclusion mentioned earlier that the angiosperm common ancestor was likely woody. Among the other lineages shown in Figure 26.25, the monocots and eudicots in particular have radiated extensively: There are now 70,000 species of monocots and 170,000 species of eudicots.

From their humble beginnings in the Cretaceous, angiosperms have diversified into more than 250,000 species, making them by far the largest group of living plants. This large group, along with fungi and nonflowering plants, has enormous ecological and evolutionary effects on other species.

CONCEPT CHECK 26.4

1. What features not present in seedless plants have contributed to the enormous success of seed plants on land?
2. Explain why Darwin called the origin of angiosperms an "abominable mystery," and describe what has been learned from fossil evidence and phylogenetic analyses.
3. **MAKE CONNECTIONS** Does the hypothesis that living gymnosperms and angiosperms are sister clades imply that they originated at the same time (see Figure 20.5)?

For suggested answers, see Appendix A.

CONCEPT 26.5

Land plants and fungi fundamentally changed chemical cycling and biotic interactions

Throughout Unit Four, we are highlighting major steps in the evolutionary history of life. We have focused on great waves of adaptive radiation, such as the metabolic diversification of prokaryotes (Chapter 24) and the rise in structural diversity that followed the origin of eukaryotes (Chapter 25). In this chapter, we've examined another major step in the history of life: the colonization of land by plants and fungi. Let's now explore how the colonization of land has altered the physical environment and the organisms that live there.

Physical Environment and Chemical Cycling

Fungi and plants have profound effects on the physical environment. Consider a **lichen**, a symbiotic association between a fungus and a photosynthetic microorganism. 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 altering it,

Star anise. Some of the shrubs and small trees in this genus (*Illicium*) are native to southeast Asia, others to the southeastern United States. Living species in the genus probably descended from ancestors whose populations were separated by continental drift.

Magnoliids. This clade consists of about 8,000 woody and herbaceous species, including such familiar and economically important plants as magnolias, laurels, avocado, cinnamon, and black pepper. The variety of southern magnolia shown here (*Magnolia grandiflora*, also called "Goliath"), has flowers that can measure up to about a foot across.

Monocots. Over 25% of extant angiosperms are monocots. This large clade includes the most important crop plants in the world today: grains such as maize, rice, and wheat. Other monocots are widely used as ornamental plants, such as the pygmy date palm (*Phoenix roebelenii*) shown at left. The monocots also include plants such as orchids, grasses, irises, and onions.

Eudicots. Nearly 70% of living flowering plants are eudicots. One example, zucchini, a subspecies of *Cucurbita pepo*, is an important crop, as are acorn squash, pumpkin, and other *C. pepo* subspecies. The eudicots also include sunflowers, roses, cacti, clovers, oaks, and a wide range of other species.

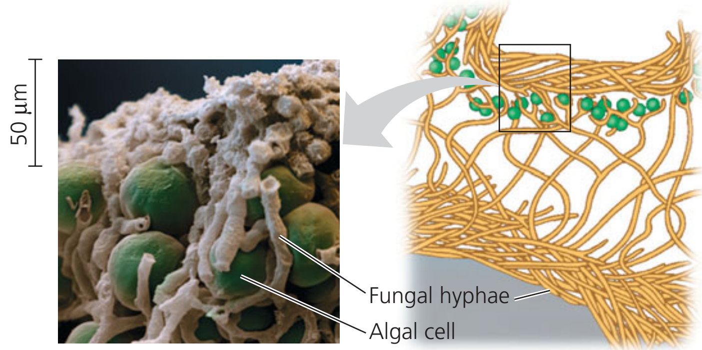
and they trap windblown soil. These processes affect the formation of soil and make it possible for plants to grow. **Figure 26.26** shows two examples of the diverse forms of lichens along with the structure of a lichen composed of a fungus and a green alga. Fossils show that lichens were on land 420 million years ago. These early lichens may have modified rocks and soil much as they do today, helping pave the way for plants.

The colonization of land by plants resulted in great changes to the physical environment. Like lichens, plants affect the formation of soil: Their roots hold the soil in place, and leaf litter and other decaying plant parts add nutrients to the soil. Plants also have altered the composition of Earth's atmosphere, perhaps most importantly by releasing oxygen to the air as a by-product of photosynthesis.

Plants and fungi also have profound effects on the cycling of chemicals in ecosystems (see Figure 1.9). This process begins when plants absorb nutrients from the physical environment. Next, those nutrients pass to organisms that eat plants. Decomposers then break down the bodies of dead organisms, thereby returning nutrients to the physical environment and completing the cycle. Fungi are well adapted as decomposers of organic material. 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 play a central role in 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, life as we know it would cease.

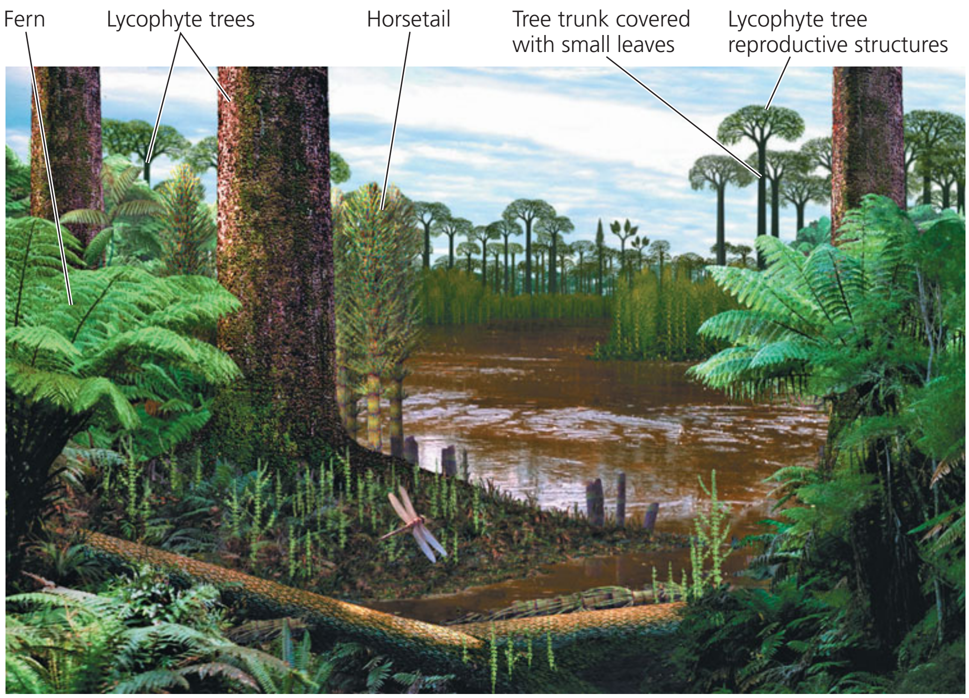
Let's take a closer look at how plants affect carbon recycling. Carbon forms the basis of the organic compounds that are essential for life. During photosynthesis, plants remove large quantities of CO_2 from the atmosphere—an action that can influence the global climate. A dramatic example occurred when seedless vascular plants first grew tall, forming the first forests about 385 million years ago **(Figure 26.27)**. With the evolution of vascular tissue, roots, and leaves, these plants accelerated their rate of photosynthesis, greatly increasing the removal of CO_2 from the atmosphere. Scientists estimate that CO_2 levels dropped by up to a factor of five during the Carboniferous (359–299 million years ago), causing global cooling that resulted in widespread glacier formation. Today, plants continue to influence carbon cycling and thereby both the global climate and the extent of global climate change (see Chapters 42 and 43).

(a) Two common lichen growth forms



(b) Anatomy of a lichen involving an ascomycete fungus and an alga

▲ **Figure 26.26 Lichens.** Often found growing on rocks or rotting logs, lichens are a symbiotic association between a fungus and a photosynthetic microorganism (a green alga or a cyanobacterium).



▲ **Figure 26.27 Artist's conception of a Carboniferous forest based on fossil evidence.** In addition to plants, animals, including giant dragonflies like the one in the foreground, also thrived in Carboniferous forests.

Biotic Interactions

The colonization of land by plants and fungi also had a dramatic effect on interactions between members of different species. Such biotic interactions include those in which both species benefit (mutualism) and those in which one species benefits while the other is harmed (as when a parasite feeds on its host).

Plants and fungi had such large effects on biotic interactions because their presence on land increased the availability of energy and nutrients for other organisms. For example, during photosynthesis, plants convert light energy to the chemical energy of food. That chemical energy supports all life on land, either directly (as when an insect eats a plant leaf) or indirectly (as when a bird eats an insect that ate a plant). Likewise, nitrogen and other nutrients are first absorbed by plants and then passed to organisms that eat plants; ultimately, these nutrients are returned to the environment by the actions of fungi and other decomposers. If plants and fungi had not colonized land, biotic interactions would still result in the transfer of energy and nutrients, but those transfers would likely occur on a much smaller scale, such as that of the "green slime" mentioned earlier in the chapter.

The previous paragraphs describe the big picture of how plants and fungi have affected biotic interactions. We'll close the chapter with several specific examples.

▼ **Figure 26.28 Inquiry**

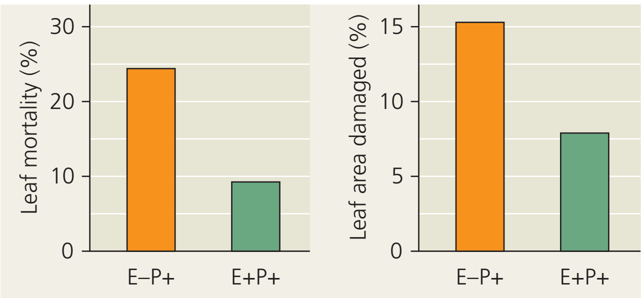
Do endophytes benefit a woody plant?

Experiment Endophytes are symbiotic fungi found within the bodies of all plants examined to date. Researchers tested whether 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. Endophytes were added to the leaves of some cacao seedlings, but not others. (In cacao, 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 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.

Endophyte not present; pathogen present (E–P+)

Both endophyte and pathogen present (E+P+)



Conclusion Endophytes appear to benefit cacao trees by reducing the leaf mortality and damage caused by *Phytophthora*.

Source A. E. Arnold et al., Fungal endophytes limit pathogen damage in a tropical tree, *Proceedings of the National Academy of Sciences* 100:15649–15654 (2003).

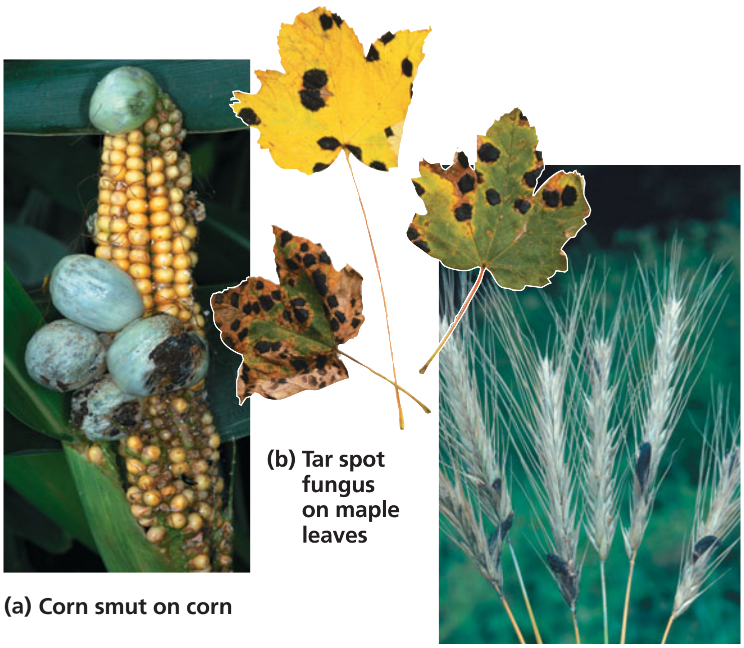
WHAT IF? The researchers also performed control treatments. Suggest two controls they might have used, and explain how each would be helpful in interpreting the results described here.

Fungi as Mutualists and Pathogens

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, with different species living as decomposers, mutualists, or parasites. Having already described the importance of fungi as decomposers, we'll focus here on mutualism and parasitism.

Mutualistic fungi absorb nutrients from a host organism, but they reciprocate with actions that benefit the host—as we already saw for the enormously important mycorrhizal associations that fungi form with most vascular plants. In addition, all plant species studied to date appear to harbor symbiotic **endophytes**, fungi that live inside leaves or other plant parts without causing harm. Endophytes have been shown to benefit certain grasses by making toxins that deter herbivores or by increasing host plant tolerance of heat, drought, or heavy metals. Seeking to discover how endophytes affect a woody plant, researchers tested whether leaf endophytes benefit seedlings of the cacao tree, *Theobroma cacao* **(Figure 26.28)**. Their findings show that the endophytes of woody flowering plants can play an important role in defending against pathogens.

Parasitic fungi also absorb nutrients from the cells of living hosts, but they provide no benefits in return **(Figure 26.29)**.



(a) Corn smut on corn

(c) Ergots on rye

▲ **Figure 26.29 Examples of fungal diseases of plants.** About 30% of the 100,000 known species of fungi make a living as parasites or pathogens, mostly of plants.

Some parasitic fungi are pathogenic, including many species that cause diseases in plants. For example, *Cryphonectria parasitica*, the ascomycete fungus that causes chestnut blight, dramatically changed the landscape of the northeastern United States. Accidentally introduced on trees imported from Asia in the early 1900s, spores of the fungus enter cracks in the bark of American chestnut trees and produce hyphae, killing the tree. The once-common chestnuts now survive mainly as sprouts from the stumps of former trees.

Plant-Animal Interactions

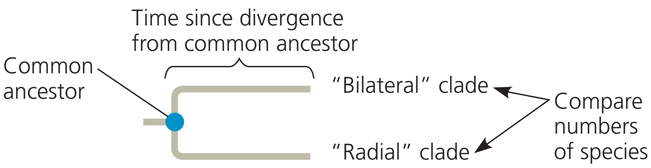
Plants and animals have interacted for hundreds of millions of years, and those interactions have led to evolutionary change. For example, herbivores can reduce a plant's reproductive success by eating its roots, leaves, or seeds. As a result, if an effective defense against herbivores originates in a group of plants, those plants may be favored by natural selection—as will any herbivores that can overcome this new defense.

Interactions between plants and animals also may have affected the rates at which new species form. Consider the impact of flower shape, which can be symmetric in one direction only (*bilateral symmetry*) or symmetric in all directions (*radial symmetry*). On a flower with bilateral symmetry, an insect pollinator may only be able to enter the flower from a certain direction. This constraint can make it more likely that as an insect moves from flower to flower, 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.

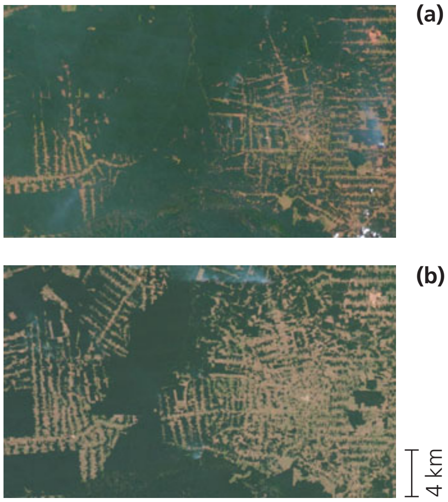
Bilateral symmetry

Radial symmetry

Such specificity of pollen transfer tends to reduce gene flow between diverging populations and hence could lead to increased rates of plant speciation in plants with bilateral symmetry. This hypothesis can be tested using the approach illustrated in this diagram:



A key step 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 such pairs of closely related "bilateral" and "radial" clades. On average, the clade with bilaterally symmetric flowers had nearly 2,400 more species than did its closely related clade with radially symmetric flowers. This result suggests that flower shape can affect the rate at which new species form—perhaps because of how flower shape affects the behavior of insect pollinators. Overall, the effects of plant-pollinator interactions are thought to have contributed



(a) A satellite image from 2000 shows clear-cut areas in Brazil (brown) surrounded by dense tropical forest (green).

(b) By 2009, much more of this same tropical forest had been cut down.

▲ **Figure 26.30 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.

to the diversification and increasing dominance of flowering plants in the Cretaceous period.

While angiosperms continue to dominate the communities of today, they and other plant groups are being threatened by the exploding human population and its demand for space and resources. 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 55,000 km^2 (14 million acres) of tropical rain forest are cleared each year **(Figure 26.30)**, a rate that would completely eliminate the remaining 11 million km^2 of tropical forests in 200 years. 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 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 changing the evolutionary history of life—including that of the animals, the group we'll turn to in Chapter 27.

CONCEPT CHECK 26.5

1. Describe how terrestrial fungi and land plants have affected the physical environment.
2. Discuss the importance of fungi as mutualists and parasites.
3. **MAKE CONNECTIONS** Figure 1.9 illustrates the transfer of energy and matter in ecosystems. Draw a simple diagram of energy flow and chemical cycling in a terrestrial ecosystem; circle the steps that were affected by the colonization of land by plants and fungi.
4. **WHAT IF?** Explain why researchers testing whether flower shape (bilateral versus radial) affected speciation rates only analyzed cases in which a bilateral clade shared an immediate common ancestor with a radial clade.

For suggested answers, see Appendix A.

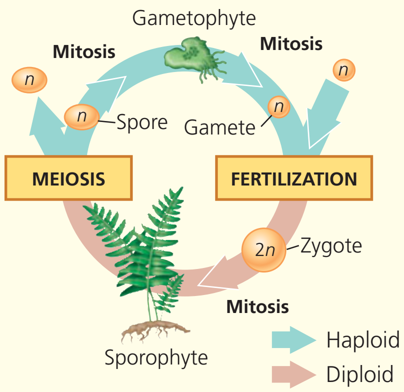
26 Chapter Review

SUMMARY OF KEY CONCEPTS

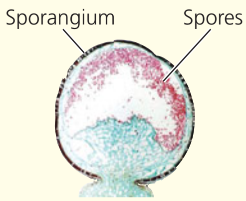
CONCEPT 26.1

Fossils show that plants colonized land more than 470 million years ago (pp. 505–508)

- Morphological and biochemical traits, as well as similarities in nuclear and chloroplast gene sequences, indicate that land plants arose from charophyte green algae.
- 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 land plants from charophytes, their closest algal relatives, include **apical meristems**, **cuticles**, **stomata**, and the two shown here:



1 **Alternation of generations**



2 **Walled spores in sporangia**

- Fossil evidence indicates that plants were inhabiting land by 470 million years ago. By 400 million years ago, a diverse assemblage of fossil plant species lived on land, some of which had specialized tissues for water transport, stomata, and branched sporophytes.

? *The oldest fossil representing a large structure from a plant is 425 million years old, yet scientists think that plants colonized land 470 million years ago. What evidence supports this idea?*

CONCEPT 26.2

Fungi played an essential role in the colonization of land (pp. 508–513)

- All **fungi** are heterotrophs that acquire nutrients by absorption. Many fungi secrete enzymes that break down complex molecules to smaller molecules that can be absorbed.
- The cell walls of fungi are strengthened by **chitin**, a strong but flexible polysaccharide; these strong cell walls enable the cell to absorb nutrients and water without bursting.
- 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.
- Fungi typically propagate themselves by producing **spores**, either sexually or asexually. Spores can be transported by wind or water; if they are deposited in a moist place that has food, they germinate, producing new mycelia.
- Although fungi likely colonized land before plants, the earliest fossils of fungi date to 460 million years ago. Once on land, some fungi formed mycorrhizal associations with early plants—a symbiosis that probably helped plants without roots to colonize land.
- Molecular data show that fungi arose from a single-celled protist and are more closely related to animals than to plants or most other eukaryotes. Since colonizing land, fungi have radiated into a diverse set of lineages.

? *Explain how the morphology of multicellular fungi affects the efficiency of nutrient absorption and may have played a role in the colonization of land by plants.*

CONCEPT 26.3

Early land plants radiated into a diverse set of lineages (pp. 513–516)

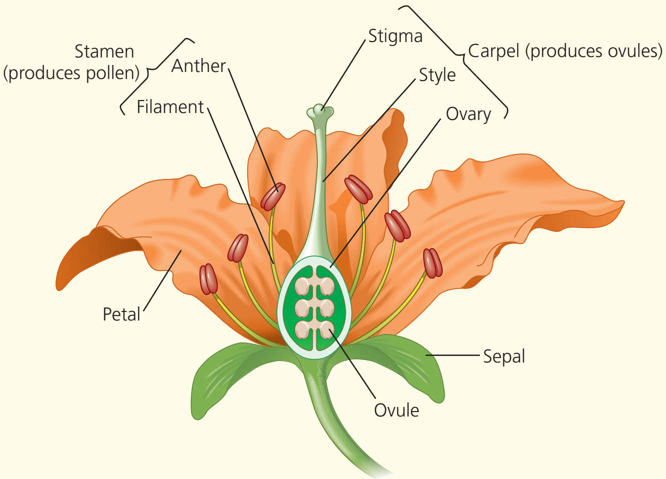
- The three extant phyla of nonvascular plants, or **bryophytes**—liverworts, mosses, and hornworts—are the earliest-diverging plant lineages.
- In bryophytes, the dominant generation consists of haploid **gametophytes**, such as those that make up a carpet of moss. The flagellated sperm require a film of water to travel to the eggs.
- Fossils of the forerunners of today's vascular plants date back 425–420 million years and show that these small plants lacked seeds but had independent, branching sporophytes and a well-developed vascular system.
- Over time, other derived traits of living vascular plants arose, such as a life cycle with dominant sporophytes; lignified vascular tissue; and well-developed roots and leaves.
- Seedless vascular plants formed the first forests about 385 million years ago. Today, seedless vascular plants include the **lycophytes** (club mosses and their relatives) and the **monilophytes** (ferns and their relatives).

? *What trait(s) allowed vascular plants to grow tall, and why might increased height have been advantageous?*

CONCEPT 26.4

Seeds and pollen grains are key adaptations for life on land (pp. 516–521)

- Derived traits of seed plants include **seeds** (which survive better than spores), highly reduced gametophytes (which are nourished and protected by the sporophyte), **ovules** (which house female gametophytes), and pollen (which eliminates dependency on water for fertilization).
- Seed plants originated 360 million years ago. Living seed plants can be divided into two monophyletic groups: **gymnosperms** and **angiosperms**. Gymnosperms appear early in the seed plant fossil record and dominated many terrestrial ecosystems until angiosperms (flowering plants) began to replace them 100 million years ago.
- **Flowers** typically have four whorls of modified leaves: **sepals, petals, stamens**, and **carpels**. Ovaries ripen into **fruits**, which often carry seeds by wind, water, or animals to new locations.



Flower anatomy

- Angiosperms arose and diversified greatly during the Cretaceous period. Fossils and phylogenetic analyses offer insights into the origin of flowering plants, which today are by far the largest group of extant land plants. The two most diverse angiosperm clades are monocots and eudicots.

? *Summarize fossil and phylogenetic evidence that suggests that the angiosperm common ancestor was likely woody.*

CONCEPT 26.5

Land plants and fungi fundamentally changed chemical cycling and biotic interactions (pp. 521–524)

- **Lichens** and plants affect soil formation. Plants also alter the composition of Earth's atmosphere by releasing oxygen to the air as a by-product of photosynthesis.
- Plants play a central role in chemical cycling by absorbing nutrients from the physical environment; those nutrients then pass to organisms that eat plants. Fungal decomposers break down the bodies of dead organisms; this returns nutrients to the physical environment, completing the cycle.
- Since colonizing land, the activities of plants and fungi have altered biotic interactions by increasing the availability of energy and nutrients for other organisms.
- Fungi play key ecological roles as decomposers, mutualists (such as **endophytes** that help protect plants from herbivores and pathogens), and parasites.
- Interactions between plants and animals have led to natural selection in plant and animal populations and may have affected speciation rates. Destruction of habitat threatens the extinction of many plant species and the animal species they support.

? *Summarize how plants and fungi have increased the availability of energy and nutrients for other organisms, and explain how this affects biotic interactions.*

TEST YOUR UNDERSTANDING

Level 1: Knowledge/Comprehension

1. *All* fungi are
   a. symbiotic
   b. heterotrophic
   c. flagellated
   d. pathogenic
   e. decomposers

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. multicellularity
   d. sexual reproduction
   e. alternation of generations

3. Identify each of the following structures as haploid or diploid.
   a. sporophyte
   b. spore
   c. gametophyte
   d. zygote
   e. sperm

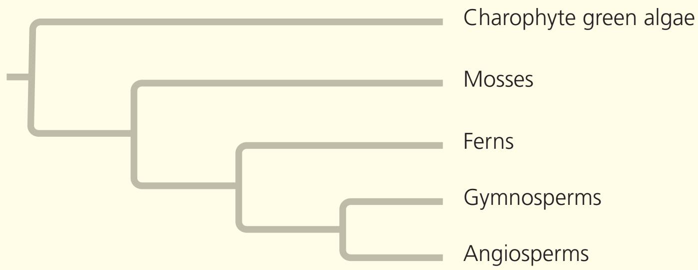
4. A fruit is usually
   a. a mature ovary.
   b. a thickened style.
   c. an enlarged ovule.
   d. a modified root.
   e. a mature female gametophyte.

5. Among the organisms listed here, which are thought to be the closest relatives of fungi?
   a. slime molds
   b. vascular plants
   c. animals
   d. brown algae
   e. mosses

Level 2: Application/Analysis

6. The adaptive advantage associated with the filamentous nature of fungal mycelia is primarily related to
   a. the ability to form haustoria and parasitize other organisms.
   b. avoiding sexual reproduction until the environment changes.
   c. the potential to inhabit almost all terrestrial habitats.
   d. the increased probability of contact between different mating types.
   e. an extensive surface area well suited for invasive growth and absorptive nutrition.

7. **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



8. **SCIENTIFIC INQUIRY**
   DRAW IT The grass *Dichanthelium languinosum* lives in hot soils and houses fungi of the genus *Curvularia* as endophytes. Researchers performed field experiments to test the impact of *Curvularia* on the heat tolerance of this grass. They grew plants without (E−) and with (E+) *Curvularia* endophytes in soils of different temperatures and measured plant mass and the number of new shoots the plants produced. Draw a bar graph of the results for plant mass versus temperature and interpret it.

Soil Temp.	*Curvularia* Presence	Plant Mass (g)	Number 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

Source R. S. Redman et al., *Science* 298:1581 (2002).

Level 3: Synthesis/Evaluation

9. FOCUS ON EVOLUTION
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 Chapter 23). 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?

10. FOCUS ON INTERACTIONS
Giant lycophyte trees of Earth's early forests (see Figure 26.27) 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 in which they grew may have affected interactions among small plants growing beneath the tall ones.

For selected answers, see Appendix A.

27 The Rise of Animal Diversity

KEY CONCEPTS

27.1 Animals originated more than 700 million years ago

27.2 The diversity of large animals increased dramatically during the "Cambrian explosion"

27.3 Diverse animal groups radiated in aquatic environments

27.4 Several animal groups had features that facilitated their colonization of land

27.5 Animals have transformed ecosystems and altered the course of evolution

▼ **Figure 27.1 What adaptations make a chameleon a fearsome predator?**

OVERVIEW

Life Becomes Dangerous

Although slow moving on its feet, the chameleon in **Figure 27.1** can wield its long, sticky tongue with blinding speed to capture unsuspecting prey. Other animals overwhelm their prey using their strength, speed, or toxins, while still others build traps or blend into their surroundings, enabling them to capture unwary prey. And hunting animals are not the only ones that pose a threat to other organisms. Herbivorous animals can strip the plants they eat bare of leaves or seeds, while parasitic animals weaken their hosts by consuming their tissues or body fluids.

As these examples suggest, animals can make life dangerous for the organisms around them. Most animals are mobile and can detect, capture, and eat other organisms—including those that are mobile themselves and can flee from attack. Indeed, all but the simplest animals have specialized muscle and nerve cells that allow them to move and respond rapidly to changing environmental conditions. Most animals also have a complete digestive tract, an efficient digestive system that has a mouth at one end and an anus at the other. Together, their mobility, nervous system, and digestive tract, accompanied by often complex behaviors, make animals highly effective eating machines.

Animals are so integral to our lives today that it is difficult to imagine what Earth would be like without animals. The fossil record, however, paints an intriguing picture. Large eukaryotes were once soft-bodied and lived in a relatively safe world—until the appearance of animals changed everything. In this chapter, we'll examine how animals have evolved over time and influenced the world around them.

CONCEPT 27.1

Animals originated more than 700 million years ago

Current evidence indicates that animals evolved from single-celled eukaryotes similar to present-day choanoflagellates (see Chapter 25). These early animals have given rise to a vast diversity of living animal species: To date, biologists have named more than 1.3 million species, and estimates of the actual number

(a) *Dickinsonia costata* (taxonomic affiliation unknown)

(b) The fossil mollusc *Kimberella*

▲ **Figure 27.2 Ediacaran fossils.** Fossils dating to about 560 million years ago include the earliest macroscopic fossils of animals, including these two species. Earlier members of the Ediacaran biota include the alga *Doushantuophyton* (see Figure 25.2).

run far higher—nearly 8 million species according to one recent study. When did this diverse group originate?

Fossil and Molecular Evidence

Researchers have unearthed 710-million-year-old sediments containing the fossilized remains of steroids that today are primarily produced by a particular group of sponges. Hence, 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 (living) animal species lived about 770 million years ago.

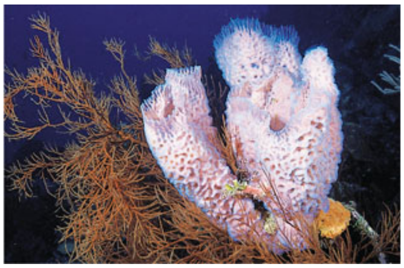
Despite the data from molecular clocks and fossil steroids indicating an earlier origin, the first generally accepted macroscopic fossils of animals date from about 560 million years ago **(Figure 27.2)**. These fossils are members of an early group of soft-bodied multicellular eukaryotes known collectively as the **Ediacaran biota**. The name comes from the Ediacara Hills of Australia, where fossils of these organisms were first discovered. Similar fossils have since been found on other continents. Among the Ediacaran fossils that resemble animals, some may be sponges, while others may be related to living cnidarians (sea anemones and their relatives) and molluscs (snails and their relatives). Still others are difficult to classify, as they do not seem to be closely related to any living animals or algae.

Early-Diverging Animal Groups

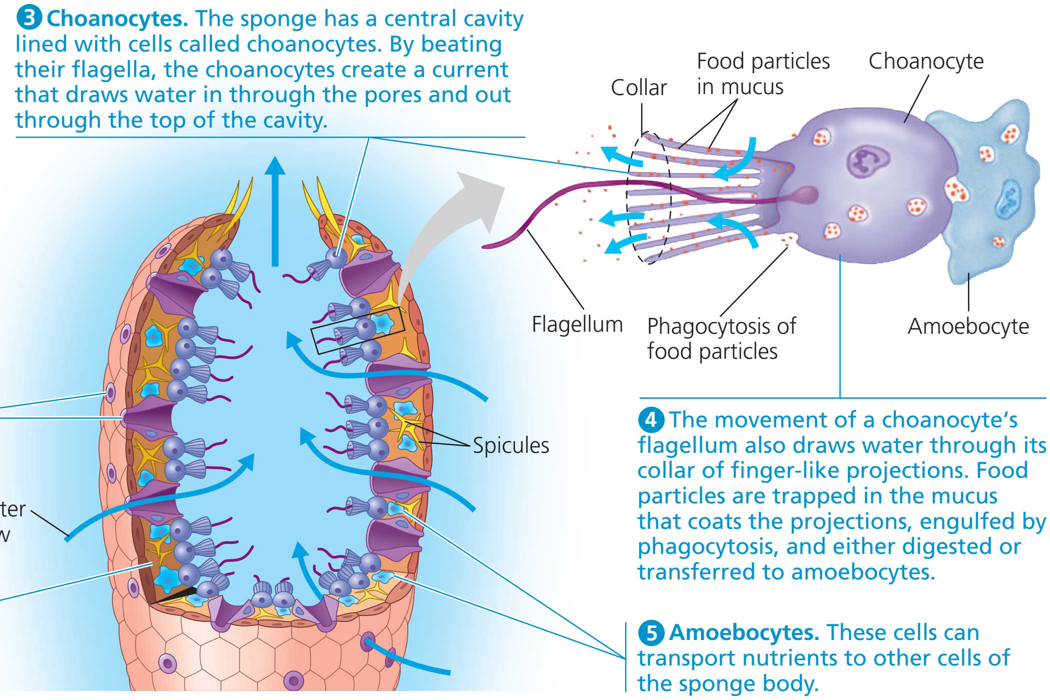
As the first animals evolved over time, their descendants gave rise to several early-diverging groups, two of which we'll discuss here: sponges and cnidarians.

Sponges

Animals in the phylum Porifera are known informally as sponges **(Figure 27.3)**. (Recent molecular studies indicate that sponges are monophyletic, and that is the phylogeny we present



Azure vase sponge (*Callyspongia plicifera*)



▲ **Figure 27.3 Anatomy of a sponge.**

here; this remains under debate, however, as some studies suggest that sponges are paraphyletic.) 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 water as they draw it through their body (see Figure 27.3).

Sponges represent a lineage that originates near the root of the phylogenetic tree of animals; 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. However, the sponge body does contain several different cell types. For example, the interior of the body is lined with 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. Choanocytes resemble the cells of choanoflagellates, a finding that is consistent with the similarities between the DNA sequences of sponges and those of choanoflagellates. Together, these results suggest that animals evolved from a choanoflagellate-like ancestor (see Figure 25.7). Sponges also have mobile cells called **amoebocytes**, named for their use of pseudopodia. As these cells move through the sponge body, they take up food from the surrounding water and from choanocytes, digest it, and carry nutrients to other cells.

Cnidarians

All animals except sponges and a few other groups are *eumetazoans* ("true animals"), members of a clade of animals that have tissues. One of the oldest lineages in this clade is the phylum Cnidaria, which originated about 680 million years ago according to molecular clock analyses. Cnidarians have diversified into a wide range of sessile and motile forms, including hydrozoans, jellies, and sea anemones **(Figure 27.4)**.

The basic morphology 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. Cnidarians are carnivores that often use tentacles arranged in a ring around their mouth to capture prey and pass the food into their gastrovascular cavity. Enzymes are then secreted into the cavity, 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.

Muscles and nerves occur in their simplest forms in cnidarians. Movements are coordinated by a noncentralized nerve net. Cnidarians have no brain, and the nerve net is associated with sensory structures distributed around the body. Thus, the animal can detect and respond to stimuli from all directions.

CONCEPT CHECK 27.1

1. Summarize fossil and DNA evidence documenting the origin and early diversification of animals.
2. **WHAT IF?** Suppose the most recent common ancestor of choanoflagellates and animals lived 900 million years ago. If extant choanoflagellates arose 890 million years ago, would extant animals also have been alive at that time? Explain.

For suggested answers, see Appendix A.

(a) Hydrozoa. Some species, such as this one, live as colonial polyps.

(b) Scyphozoa. Many jellies (commonly called jellyfish) are bioluminescent. Some species stun their prey with specialized stinging cells called nematocysts located on their tentacles.

(c) Anthozoa. Sea anemones and other anthozoans exist only as polyps. Many anthozoans form symbiotic relationships with photosynthetic algae.

▲ **Figure 27.4 Major groups of cnidarians.**

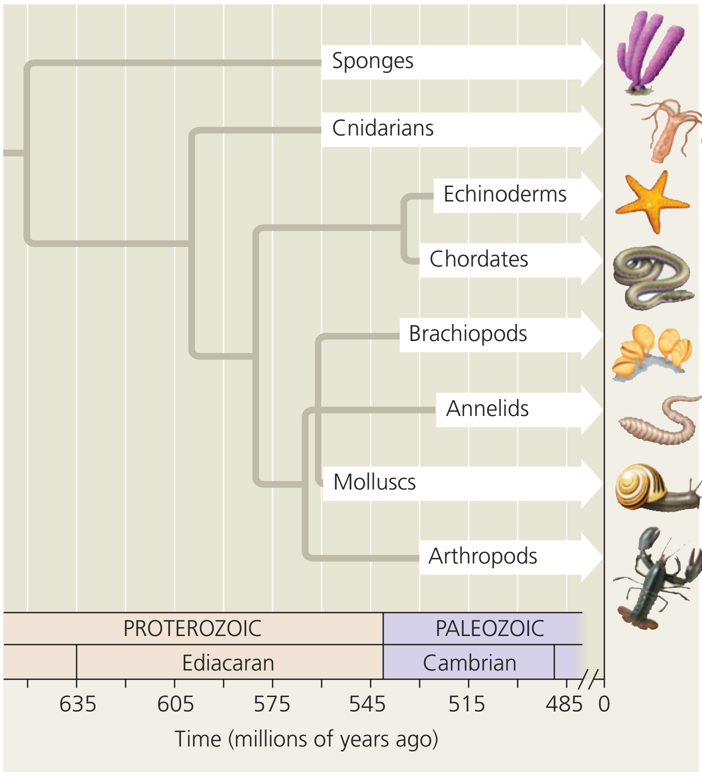
CONCEPT 27.2

The diversity of large animals increased dramatically during the "Cambrian explosion"

As we've seen, the oldest fossils of large animals date to 560 million years ago and include members of just a few extant groups—sponges, cnidarians, and molluscs. In fossils formed in the early Cambrian period (between 535 and 525 million years ago), large forms of many other present-day animal phyla suddenly appear, a phenomenon referred to as the **Cambrian explosion**. What factors may have spurred this rapid (in geologic terms) diversification?

Evolutionary Change in the Cambrian Explosion

Strata formed during the Cambrian explosion contain the oldest fossils of about half of all extant animal phyla, including the first arthropods, chordates, and echinoderms **(Figure 27.5)**. Many of these fossils, which include the first animals with hard, mineralized skeletons, look very different from most living animals **(Figure 27.6)**. Even so, paleontologists have established that these



▲ **Figure 27.5 Appearance of selected animal groups.** The white bars indicate earliest appearances of these animal groups in the fossil record.

DRAW IT *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?*

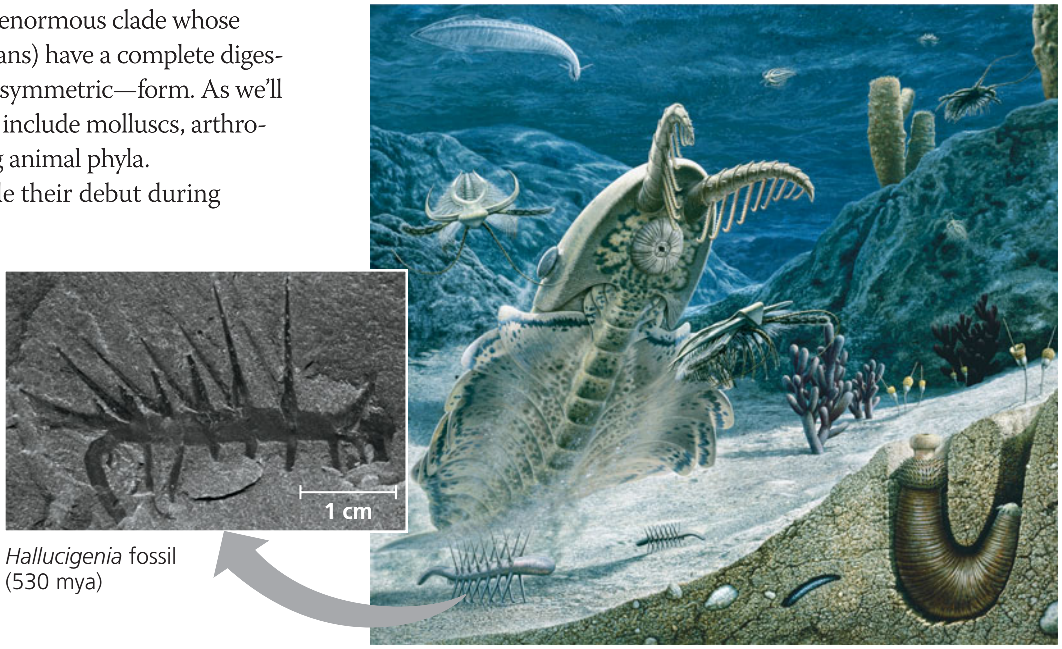
Cambrian fossils are members of extant animal phyla, or at least are close relatives. In particular, most of the fossils from the Cambrian explosion are of **bilaterians**, an enormous clade whose members (unlike sponges and cnidarians) have a complete digestive tract and a two-sided—bilaterally symmetric—form. As we'll discuss later in the chapter, bilaterians include molluscs, arthropods, chordates, and most other living animal phyla.

Entirely new sorts of animals made their debut during the Cambrian explosion. Previously, virtually all large animals were soft-bodied. In addition, the fossils of large pre-Cambrian animals reveal little evidence of predation. Instead, these animals seem to have been grazers (feeding on mats of algae and bacteria), filter feeders, or scavengers, not hunters. 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 (see Figure 27.6). These and other changes set the stage for many of the key events in the history of life over the last 500 million years.

The increase in the diversity of large animals during the Cambrian explosion was accompanied by a decline in the diversity of Ediacaran life-forms. What caused these trends? Fossil evidence suggests that during the Cambrian period, predators acquired novel adaptations, such as forms of locomotion that helped them catch prey, while 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 the origin of *Hox* genes (see Concept 23.3) and other genetic changes affecting the regulation of developmental genes facilitated the evolution of new body forms. These hypotheses are not mutually exclusive, however; predator-prey relationships, atmospheric changes, and changes in the regulation of development may each have played a role.

Dating the Origin of Bilaterians

Although the radiation of bilaterians during the Cambrian explosion had an enormous impact on life on Earth, it is possible that many animal phyla originated long before that time. As we've seen, molecular clock analyses suggest that two early-diverging groups, sponges and cnidarians, had evolved by



Hallucigenia fossil (530 mya)

▲ **Figure 27.6 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* (arthropod swimming at left), *Anomalocaris* (large animal with anterior grasping limbs and a circular mouth), and *Hallucigenia* (animals with toothpick-like spikes on the seafloor and in inset).

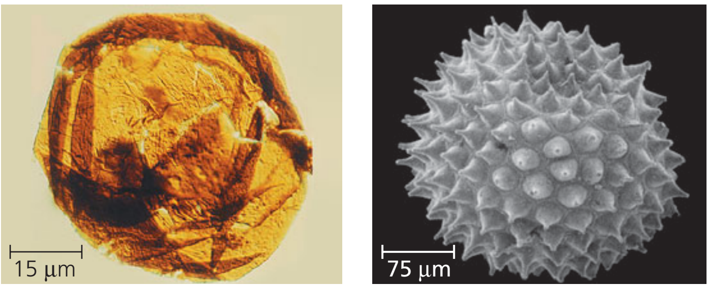
700–680 million years ago. Molecular estimates also suggest that bilaterians had evolved by 670 million years ago—135 million years *before* the Cambrian explosion.

Turning to the fossil record, fossil steroids corroborate the molecular dates for the origin of sponges. However, no fossil bilaterians are close in age to the molecular clock estimates for when this group originated. The oldest fossil bilaterian is the mollusc *Kimberella* (see Figure 27.2), which lived 560 million years ago. Thus, the fossil evidence differs from molecular clock estimates by more than 100 million years.

Seeking to resolve this discrepancy, researchers have taken a closer look at the fossil record from the Ediacaran period (635–542 million years ago). Prior to the Ediacaran, eukaryotes were microscopic and smooth-walled, and such forms appeared in the fossil record for hundreds of millions of years **(Figure 27.7a)**. Then eukaryotic life changed dramatically. Some eukaryotic lineages gave rise to large organisms, such as the 600-million-year-old alga shown in Figure 25.2. Organisms in other eukaryotic lineages remained relatively small, but defensive structures such as spines began to appear on their outer surfaces **(Figure 27.7b)**. Additional fossil evidence shows that such well-defended eukaryotes originated more rapidly and persisted in the fossil record for shorter periods of time than did their smooth-walled, pre-Ediacaran counterparts.

What triggered these dramatic changes? Recall from the chapter opening that living animals are dangerous feeding machines because of their mobility, nervous system, and efficient digestive tract. Most bilaterians have these features, and early bilaterians may have decimated populations of the small, soft-bodied organisms on which they fed. Thus, the feeding activities of early bilaterians may have resulted in natural selection for increased size or new defensive structures in the organisms that they ate—exactly the change seen in the fossil record during the Ediacaran period.

Overall, the fossil record and molecular clock results suggest that bilaterians arose sometime between 670 and 635 million years ago. Possibly aided by a later rise in the atmospheric concentration of oxygen, these early bilaterians then diversified explosively during the Cambrian and beyond.



(a) *Valeria* (800 mya): roughly spherical, no structural defenses, soft-bodied

(b) Spiny acritarch (575 mya): about five times larger than *Valeria* and covered in hard spines

▲ **Figure 27.7 Indirect evidence of the appearance of bilaterians?** The rise in the fossil record of larger, well-defended eukaryotes during the Ediacaran period (635-542 million years ago) suggests that bilaterian animals with a complete digestive tract may have originated by that time.

CONCEPT CHECK 27.2

1. What is the "Cambrian explosion," and why is it significant?
2. **WHAT IF?** Suppose a well-defended prey species arose that was difficult for predators to catch or eat. How might this affect ongoing evolutionary changes in predator and prey populations?

For suggested answers, see Appendix A.

CONCEPT 27.3

Diverse animal groups radiated in aquatic environments

By the end of the Cambrian explosion, many of the big steps in animal evolution were well under way. Animals with legs or leg-like appendages walked on the ocean floor, and worms burrowed through the sediments. Swimming in the waters above were predators that used sharp claws and mandibles to capture and break apart their prey. Other animals had protective spikes or armor, as well as modified mouthparts that enabled their bearers to filter food from the water.

As these examples suggest, the animals in early Cambrian oceans were very diverse in morphology, way of life, and taxonomic affiliation. We'll examine that diversity here, beginning with an overview of how to categorize the morphological variation found in different animal groups.

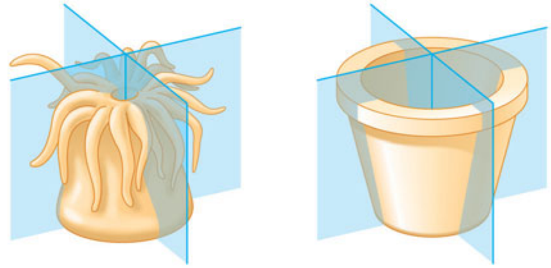
Animal Body Plans

The diversity in form of the animals that emerged from the Cambrian explosion consists of a relatively small number of major "body plans." A **body plan** is a particular set of morphological and developmental traits, integrated into a functional whole—the living animal. Note that 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. We'll focus on three aspects of animal body plans: symmetry, tissues, and body cavities.

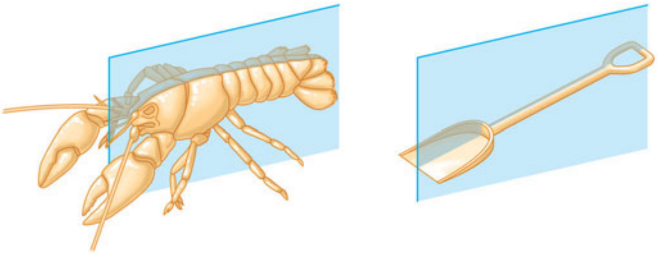
Symmetry

A basic feature of animal bodies is their type of symmetry—or absence of symmetry. (Many sponges, for example, lack symmetry altogether.) Some animals exhibit **radial symmetry**, the type of symmetry found in a flowerpot **(Figure 27.8a)**. Sea anemones, for example, have a top side (where the mouth is located) and a bottom side. But they have no front and back ends and no left and right sides.

By contrast, the two-sided symmetry of a shovel is an example of **bilateral symmetry (Figure 27.8b)**. A bilateral animal has two axes of orientation: front to back and top to bottom. Such animals have a **dorsal** (top) side and a **ventral** (bottom)



(a) Radial symmetry. A radial animal, such as a sea anemone (phylum Cnidaria), does not have a left side and a right side. Any imaginary slice through the central axis divides the animal into mirror images.



(b) Bilateral symmetry. A bilateral animal, such as a lobster (phylum Arthropoda), has a left side and a right side. Only one imaginary cut divides the animal into mirror-image halves.

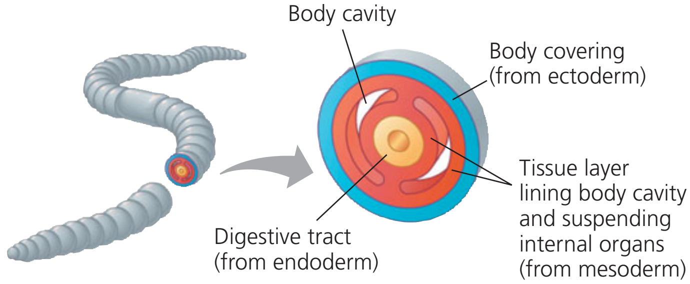
▲ **Figure 27.8 Body symmetry.** The flowerpot and shovel are included to help you remember the radial-bilateral distinction.

side, a left side and a right side, and an **anterior** (front) end and a **posterior** (back) end. Many animals with a bilaterally symmetric body plan (such as arthropods and mammals) have sensory equipment concentrated at their anterior end, including a central nervous system ("brain") in the head.

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). Their symmetry equips them to meet the environment equally well from all sides. In contrast, bilateral animals typically move actively from place to place. Most bilateral animals have a central nervous system that enables them to coordinate the complex movements involved in crawling, burrowing, flying, or swimming.

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; in animals, true tissues are isolated from other tissues by membranous layers. Sponges and a few other groups lack true tissues. In all other animals, the embryo becomes layered during development; these layers, called *germ layers*, form the various tissues and organs of the body **(Figure 27.9)**. **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, gives rise to the lining of the digestive tract (or cavity) and organs such as the liver and lungs of vertebrates.



▲ **Figure 27.9 Tissue layers in bilaterians.** The organ systems of a bilaterally symmetric animal develop from the three germ layers that form in the embryo. Blue represents tissue derived from ectoderm, red from mesoderm, and yellow from endoderm. The internal organs of most bilaterians are suspended in a "body cavity," a fluid- or air-filled space that helps protect the organs from injury.

Cnidarians and a few other animal groups have only these two germ layers. In contrast, all bilaterally symmetric animals have a third germ layer, called the **mesoderm**, which fills much of the space between the ectoderm and endoderm. In bilaterally symmetric animals, the mesoderm forms the muscles and most other organs between the digestive tract and the outer covering of the animal.

Body Cavities

Most bilaterians have a **body cavity**, a fluid- or air-filled space located between the digestive tract and the outer body wall (see Figure 27.9). This body cavity is also called a *coelom*. The inner and outer layers of tissue that surround the cavity connect and form structures that suspend the internal organs.

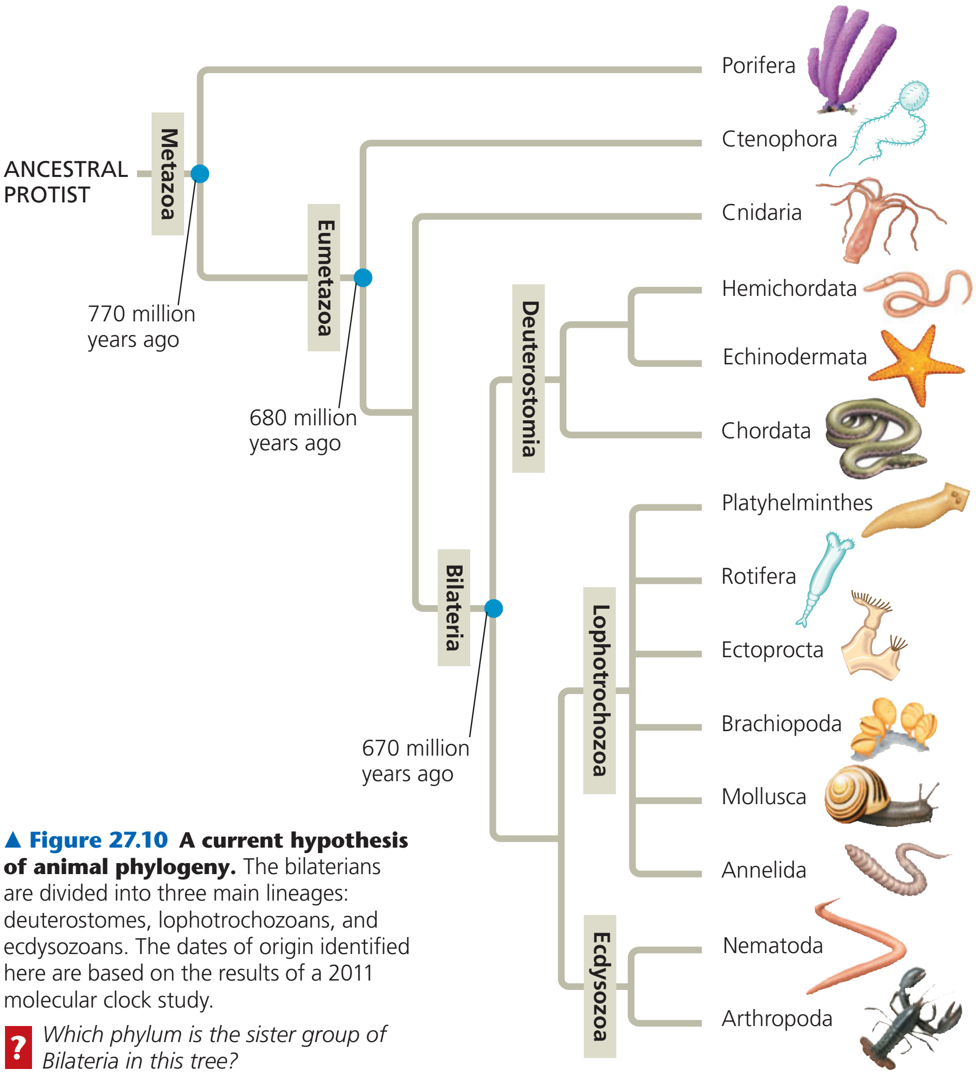
A body cavity has many functions. Its fluid cushions the suspended organs, helping to prevent internal injury. In soft-bodied bilaterians, such as earthworms, the coelom contains noncompressible fluid that acts like a skeleton against which muscles can work. The cavity also enables the internal organs to grow and move independently of the outer body wall. If it were not for your coelom, every beat of your heart or ripple of your intestine would warp your body's surface.

The Diversification of Animals

As animals radiated in 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.

Evolutionary relationships among living animals provide a helpful framework for studying the rise of animals. These relationships have been estimated using ribosomal RNA (rRNA) genes, *Hox* genes, and dozens of protein-coding nuclear genes, as well as mitochondrial genes and morphological traits. Zoologists currently recognize about three dozen animal phyla, 14 of which are shown in **Figure 27.10**. Notice how the following points are reflected in this phylogeny.

1. **All animals share a common ancestor.** Current evidence indicates that animals are monophyletic, forming



▲ **Figure 27.10 A current hypothesis of animal phylogeny.** 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 2011 molecular clock study.

? *Which phylum is the sister group of Bilateria in this tree?*

a clade called Metazoa: All extant and extinct animal lineages have descended from a common ancestor.

2. **Sponges are basal animals.** Among the extant taxa, sponges (phylum Porifera) branch from the base of the animal tree.
3. **Eumetazoa is a clade of animals with true tissues.** All animals except for sponges and a few others belong to a clade of **eumetazoans** ("true animals"). True tissues evolved in the common ancestor of living eumetazoans. Basal eumetazoans, such as ctenophores and cnidarians, have two germ layers and generally have radial symmetry.
4. **Most animal phyla belong to the clade Bilateria.** Bilateral symmetry and the presence of three 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. **Most animals are invertebrates.** The members of most animal phyla are **invertebrates**, animals that lack a backbone. Only one animal phylum, Chordata, includes **vertebrates**, animals with a backbone.

With the phylogeny in Figure 27.10 providing the overall context for the rise of animals, let's examine the bilaterian radiation in more detail; we'll begin with invertebrates.

Bilaterian Radiation I: Diverse Invertebrates

As shown in Figure 27.10, bilaterian animals have diversified into three major clades: Lophotrochozoa, Ecdysozoa, and Deuterostomia. The species in these clades dominated life in the Cambrian oceans—and initially, at least, all of these species were invertebrates.

An Overview of Invertebrate Diversity

Bilaterian invertebrates account for 95% of known animal species. 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, ranging from tiny worms with a flat body shape to species with features such as silk-spinning glands, pivoting spines, and tentacles covered with suction cups. Bilaterian invertebrates also show enormous variation in size, from microscopic organisms to organisms that can grow to 18 m long (1.5 times the length of a school bus).

The morphological diversity found in invertebrate animals is mirrored by their taxonomic diversity: There are literally millions of species of invertebrates. The vast majority of these species are members of two of the bilaterian clades that emerged from the Cambrian explosion: Lophotrochozoa and Ecdysozoa **(Figure 27.11)**. The third major bilaterian clade, Deuterostomia, also includes some invertebrates.

The seven phyla shown in Figure 27.11 serve as representatives of the great diversity of invertebrate bilaterians. Next, we'll examine the origin of one of these phyla, Arthropoda, the most species-rich (by far) of all animal groups. We focus on this group because its members were among the first animals to colonize land (see Concept 27.4).

Arthropod Origins

Zoologists estimate that there are about a billion billion (10^{18}) arthropods living on Earth. More than 1 million arthropod

▼ Figure 27.11 **Exploring the Diversity of Invertebrate Bilaterians**

Lophotrochozoa

Ectoprocts

Ectoprocta (4,500 species) Ectoprocts (also known as bryozoans) live as sessile colonies. Most species have a hard exoskeleton studded with pores; ciliated tentacles extend through the pores and trap food particles from the surrounding water.

An octopus

Mollusca (93,000 species) Molluscs (including snails, clams, squids, and octopuses) have a soft body that in many species is protected by a hard shell.

Annelida (16,500 species) Annelids, or segmented worms, are distinguished from other worms by their body segmentation. Earthworms are the most familiar annelids, but the phylum consists primarily of marine and freshwater species.

A fireworm, a marine annelid

Ecdysozoa

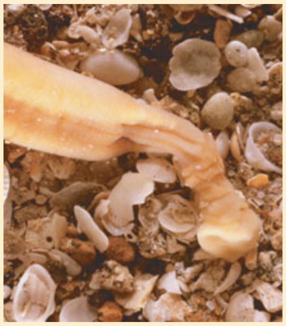
A roundworm

Nematoda (25,000 species) 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 the body.

Arthropoda (1,000,000 species) The vast majority of known animal species, including insects, millipedes, crabs, and arachnids, are arthropods. All arthropods have a segmented exoskeleton and jointed appendages.

A web-building spider (an arachnid)

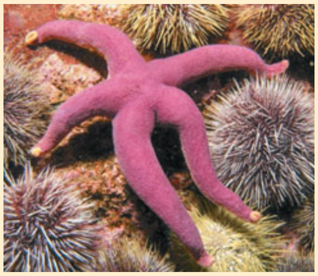
Deuterostomia



An acorn worm

Hemichordata (85 species) Hemichordates share some traits with chordates, such as gill slits and a dorsal nerve cord. The largest group of hemichordates are the acorn worms, marine animals that may grow to more than 2 m in length.

Echinodermata (7,000 species) Echinoderms, such as sea stars, sea urchins, and sand dollars, are marine animals that are bilaterally symmetric as larvae but not as adults. They move and feed using unique “tube feet” whose gripping action results from the secretion of adhesive chemicals.



Sea urchins and a sea star

species have been described, most of which are insects. In fact, two out of every three known species are arthropods, and members of this group 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.

Biologists hypothesize that the diversity and success of **arthropods** are related to their body plan—their segmented body, hard exoskeleton, and jointed appendages (*arthropod* means "jointed feet"). The earliest fossils with this body plan are from the Cambrian explosion (535–525 million years ago), indicating that the arthropods are at least that old.

Along with arthropods, the fossil record of the Cambrian explosion contains many species of *lobopods*, a group from which arthropods may have evolved. Lobopods such as *Hallucigenia* (see Figure 27.6) 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. As arthropods continued to evolve, the segments tended to fuse and become fewer, and the appendages became specialized for a variety of functions. These evolutionary changes resulted not only in great diversification but also in an efficient body plan that permits the division of labor among different body regions.

▲ **A fossil trilobite**

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, close relatives of arthropods **(Figure 27.12)**. 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 may have been driven by changes in the sequence or regulation of existing *Hox* genes (see Concept 23.3).

Bilaterian Radiation II: Aquatic Vertebrates

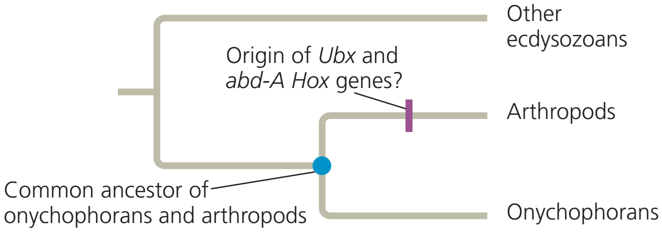
The appearance of large predatory animals about 530 million years ago and the accompanying explosive radiation of bilaterian invertebrates radically altered life in the oceans. In the face of these tumultuous events, it would have been easy to overlook certain slender, 3-cm-long creatures gliding through the water: *Myllokunmingia fengjiaoa* **(Figure 27.13)**. Although lacking armor and appendages, this ancient species was closely related to one of the most successful groups of animals ever to swim, walk, slither, or fly: the vertebrates, which derive their name from vertebrae, the series of bones that make up the backbone.

Vertebrates are members of the phylum Chordata. As seen in Figure 27.10, **chordates** are bilaterian animals, and within Bilateria, they belong to the animal clade Deuterostomia.

▼ **Figure 27.12 Inquiry**

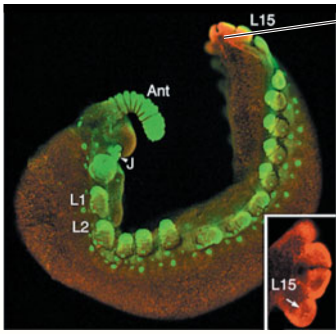
Did the arthropod body plan result from new *Hox* genes?

Experiment One hypothesis suggests that the arthropod body plan resulted from the origin (by a gene duplication event) 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 Since *A. kaputensis*, an onychophoran, has the arthropod *Hox* genes, the evolution of increased body segment diversity in arthropods must not have been related to the origin of new *Hox* genes.

Source 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? If the researchers had found that *A. kaputensis* did *not* have the *Ubx* and *abd-A Hox* genes, how would their conclusion have been affected? Explain.

▲ **Figure 27.13** ***Myllokunmingia fengjiaoa*, a 530-million-year-old chordate.**

(a) Lancelet **(b) Tunicate**

▲ **Figure 27.15 Present-day basal groups of chordates.**

Among the deuterostomes that radiated during the Cambrian, we will focus on the chordates.

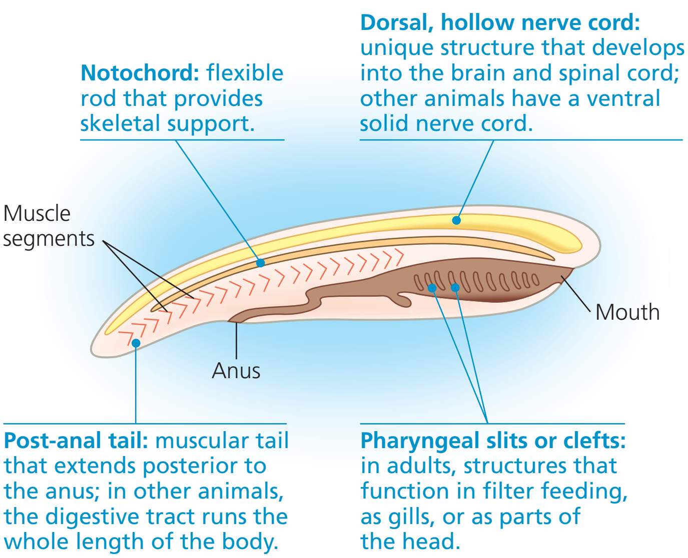
Early Chordate Evolution

All chordates share a set of derived characters, though many species possess some of these traits only during embryonic development. **Figure 27.14** illustrates four key characters of chordates: a **notochord**; a dorsal, hollow nerve cord; **pharyngeal slits** (or **pharyngeal clefts**); and a muscular, post-anal tail.

Among extant chordates, a group of blade-shaped animals called *lancelets* **(Figure 27.15a)** closely resemble the idealized chordate shown in Figure 27.14. Lancelets branch at the base of the chordate phylogenetic tree. *Tunicates* **(Figure 27.15b)**, another early diverging chordate group, also display key chordate traits, but only as larvae (adult tunicates have a highly modified body plan). 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.

After the evolution of the basic chordate body plan, another major step in early chordate evolution was the origin of vertebrates. Unlike lancelets and tunicates, vertebrates not only have a backbone, they also have a well-defined head with a brain, eyes and other sensory organs, and a skull.

Some of the fossils that formed during the Cambrian explosion 530 million years ago appear to straddle the transition to vertebrates. Some of these fossil chordates resembled lancelets, yet (unlike lancelets) they had a brain and eyes. *Myllokunmingia*, for example, not only had a brain and eyes; it also had parts of a skull surrounding its eyes and ears, making it one of the earliest chordates with a well-defined head. (The earliest "ears" were organs for maintaining balance, a function still performed by the ears of humans and other living vertebrates.)



▲ **Figure 27.14 Chordate characteristics.** All chordates possess the four highlighted structural trademarks at some point during their development.

The Rise of Vertebrates

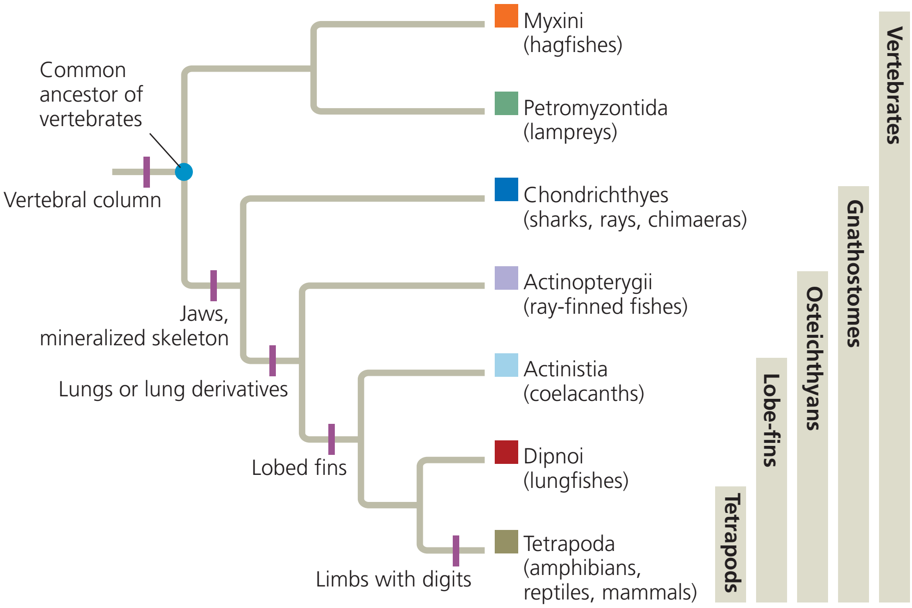
Vertebrates originated about 500 million years ago. With a more complex nervous system and a more elaborate skeleton than those of their ancestors, vertebrates became more efficient at two essential tasks: capturing food and avoiding being eaten.

Some of the earliest fossil vertebrates are of *conodonts*, soft-bodied, jawless vertebrates that hunted by impaling prey on a set of barbed hooks in their mouth. Other early vertebrates had paired fins and 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.

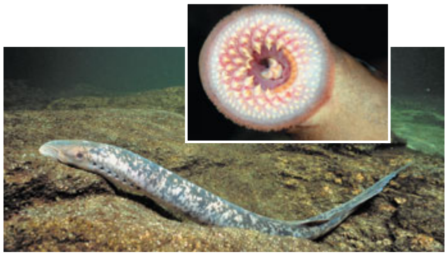
Only two lineages of jawless vertebrates survive today, the *hagfishes* and *lampreys* **(Figure 27.16)**. Living jawless vertebrates are far outnumbered by jawed vertebrates, known as **gnathostomes**. Gnathostomes appeared in the fossil record about 450 million years ago and steadily became more diverse. Their success probably resulted from a combination of anatomical features: Their paired fins and tail allowed them to

▼ Figure 27.16 Exploring Vertebrate Diversity

This phylogenetic hypothesis shows the relationships among major clades of vertebrates. Derived characters are listed for some clades; for example, only gnathostomes have a jaw. In some lineages, derived traits have been lost over time or occur in reduced form; for example, hagfishes and lampreys are vertebrates with highly reduced vertebrae.

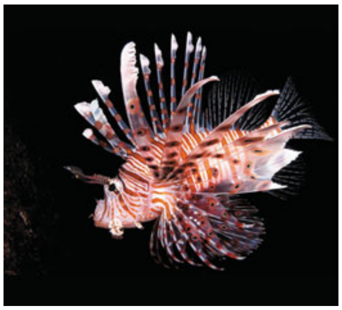


Myxini. Hagfishes (30 species) are scavengers that live and feed on the seafloor. They have slime-secreting glands that function in defense.



Petromyzontida. Most of the 35 species of lampreys are parasites that 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.

Chondrichthyes. Chondrichthyans (1,000 species) such as this black-tipped reef shark have skeletons made primarily of cartilage; the group also includes rays and chimaeras (ratfishes).



Actinopterygii. There are over 27,000 species of ray-finned fishes, including this tropical lionfish that can inject venom through its spines.

Actinistia. Coelacanths (1–2 species) were thought to have become extinct 75 million years ago until they were rediscovered in the Indian Ocean in 1938.

Dipnoi. Lungfishes (6 species) have both gills and lungs and can gulp air into their lungs.

Tetrapoda. Tetrapods (over 29,000 species) have limbs with digits; this group includes a diverse collection of amphibians, reptiles, and mammals (such as this giraffe).

swim efficiently after prey, and their jaws enabled them to grab prey or simply bite off chunks of flesh **(Figure 27.17)**.

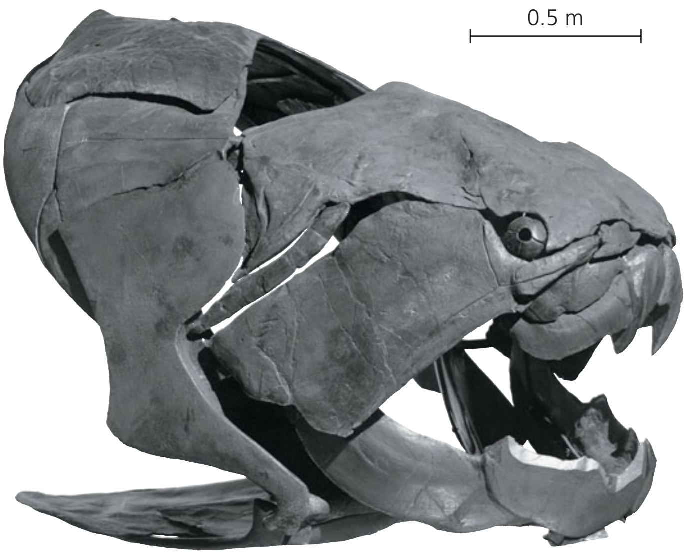
By 420 million years ago, gnathostomes had diverged into the three lineages of jawed vertebrates that survive today: chondrichthyans, ray-finned fishes, and lobe-fins. (Despite its name, this last group includes humans and other terrestrial animals with legs.)

Chondrichthyans Sharks, rays, and their relatives include some of the biggest and most successful vertebrate predators in the oceans today (see Figure 27.16). 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. There are about 1,000 species of living chondrichthyans, many of which are threatened by overfishing.

Ray-Finned Fishes The vast majority of vertebrates belong to the clade of gnathostomes called Osteichthyes. Unlike sharks and their relatives, living **osteichthyans** typically have an ossified (bony) endoskeleton; they also have lungs or lung derivatives. Nearly all the aquatic osteichthyans familiar to us are among the **ray-finned fishes** (see Figure 27.16), named for the bony rays that support their fins. Today, there are more than 27,000 species of ray-finned fishes—almost as many species as in all other vertebrate groups combined.

Lobe-Fins Along with the ray-finned fishes, the other major lineage of osteichthyans is the **lobe-fins** (see Figure 27.16). A 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 (416–359 million years ago), many lobe-fins lived in brackish waters, such as in coastal wetlands. There they may have used their lobed fins to swim and "walk" underwater across the substrate (as do some living lobe-fins).

Today, only three lineages of lobe-fins survive. Two of these lineages are the coelacanths and the lungfishes (see Figure 27.16), but the third surviving lineage of lobe-fins is far more diverse. As you'll see in the next section, these organisms adapted to life on land and gave rise to the **tetrapods**, vertebrates with limbs and digits.



▲ **Figure 27.17 Fossil of an early gnathostome.** A formidable predator, *Dunkleosteus* grew up to 10 m in length. An analysis of its jaw structure concluded that *Dunkleosteus* could exert a force of 560 kg/cm^2 (8,000 pounds per square inch) at the tip of its jaws.

CONCEPT CHECK 27.3

1. Explain what is meant by "body plan" and describe three key features of animal body plans.
2. Describe the major steps in animal evolution shown in Figure 27.10 and evaluate this statement: "The Cambrian explosion actually consists of three explosions, not one."
3. **MAKE CONNECTIONS** The bilaterian diversification in marine environments from 535 to 400 million years ago demonstrates that evolution is not goal oriented—it is not, for example, directed toward the origin of terrestrial vertebrates. Explain. (Review Concept 23.4.)

For suggested answers, see Appendix A.

CONCEPT 27.4

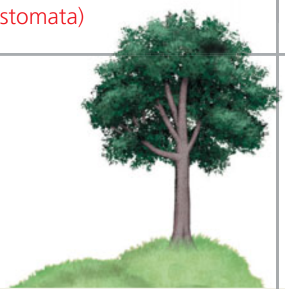
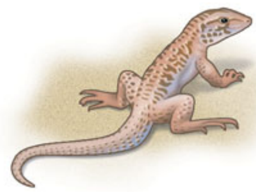
Several animal groups had features facilitating their colonization of land

Following the Cambrian explosion and its transformation of marine communities, some bilaterian animals colonized land, leading to profound changes there as well.

Early Land Animals

In contrast to plants, whose ancestors appear to have colonized land only once (see Chapter 26), members of many animal groups made the transition to terrestrial life. Arthropods, for example, invaded land multiple times, including a relatively recent event (4 million years ago) in which a crab lineage colonized the island of Jamaica. The same is true of other animal groups, such as marine snails that have given rise to terrestrial species repeatedly over the course of evolution.

Fossil evidence suggests that arthropods were among the first animals to colonize land, roughly 450 million years ago. This evidence includes fragments of arthropod remains, as well as possible millipede burrows. By 410 million years ago, well-preserved arthropod fossils from several continents indicate that millipedes, centipedes, spiders, and a variety of wingless insects all had colonized land. Vertebrates colonized land 365 million years ago, by which time early forests had also formed. By the end of the Devonian period, 360 million years ago, terrestrial animal communities were broadly similar to those of today and included predators, detritivores (animals that feed on decaying organic matter, such as plant debris), and herbivores.

		GREEN ALGA	MARINE CRUSTACEAN	AQUATIC LOBE-FIN
AQUATIC ANCESTOR				
CHARACTER	Anchoring structure	Derived (roots)	N/A	N/A
	Support structure	Derived (lignin/stems)	Ancestral	Ancestral (skeletal system) Derived (limbs)
	Internal transport	Derived (vascular system)	Ancestral	Ancestral
	Muscle/nerve cells	N/A	Ancestral	Ancestral
	Protection against desiccation	Derived (cuticle)	Ancestral	Derived (amniotic egg/scales)
	Gas exchange	Derived (stomata)	Derived (tracheal system)	Ancestral
TERRESTRIAL ORGANISM				
		LAND PLANTS	INSECTS	TERRESTRIAL VERTEBRATES

▲ **Figure 27.18 Descent with modification during the colonization of land.** This chart identifies some key characteristics that enable three major groups of terrestrial organisms—land plants, insects, and terrestrial vertebrates—to live on land. Red type indicates adaptations that have evolved since the lineages diverged from their aquatic ancestors. In land plants, most terrestrial adaptations evolved after the split. In contrast, two large clades of terrestrial animals—the insects and the vertebrates—display many ancestral characteristics that facilitated their transition to life on land.

Land animals often bear a striking resemblance to their aquatic ancestors (**Figure 27.18**). In some cases, the resemblance is so strong that it appears as if the land animals simply walked or crawled ashore, as in terrestrial crabs and snails. In other cases, more extensive changes took place, as in the vertebrate colonization of land that we'll describe shortly. But even in vertebrates, the evolutionary changes involved in the transition to terrestrial life were less extensive in animals than in plants. For example, the animals that colonized land already had well-developed skeletal, muscular, digestive, and nervous systems. Plants, in contrast, arose from a small green alga whose structure bore little resemblance to those of its descendants—the land plants that now cover Earth.

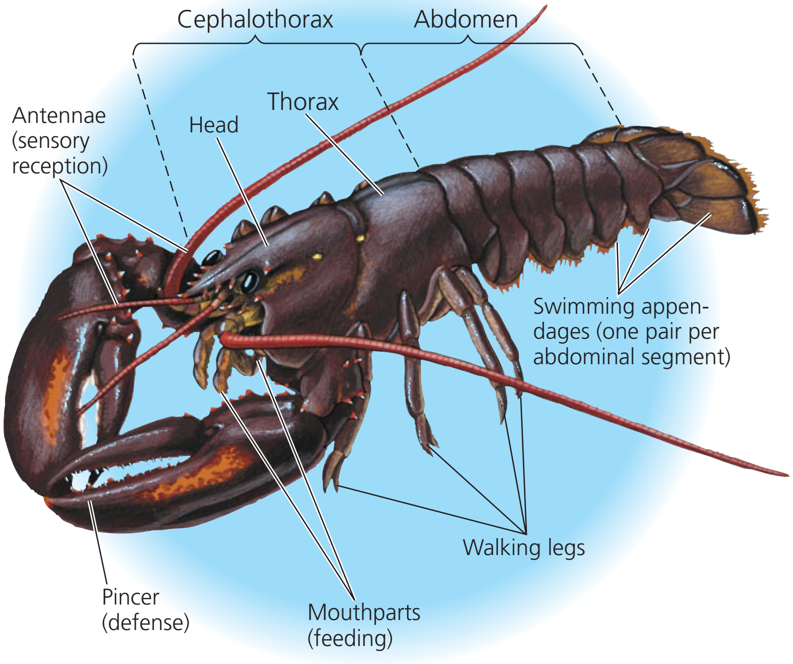
Colonization of Land by Arthropods

As mentioned earlier, terrestrial lineages have arisen in several different arthropod groups, including millipedes, spiders and their relatives, crabs, and insects. After describing general features of arthropods, we'll focus on their largest clade, the insects.

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 27.19** 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



▲ **Figure 27.19 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 characteristic is obvious only in the abdomen. The appendages (including antennae, pincers, mouthparts, walking legs, and swimming appendages) are jointed. The head bears a pair of compound (multilens) eyes, each situated on a movable stalk. The whole body, including appendages, is covered by an exoskeleton.

▶ **Lepidopterans**—moths and butterflies—undergo complete metamorphosis: The larval stage (called a caterpillar), which is specialized for eating and growing, looks completely different from the adult stage, which is specialized for dispersal and reproduction.

◀ **Hymenopterans** include ants, bees, and wasps. They undergo complete metamorphosis and most are highly social insects.

▶ **Hemipterans** include stink bugs, bed bugs, and other so-called "true bugs." They have piercing mouthparts and undergo incomplete metamorphosis: The young (nymphs) resemble the adults but are smaller and lack wings.

▲ **Figure 27.20 Insect diversity.**

appendages. Later, the exoskeleton enabled some 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.

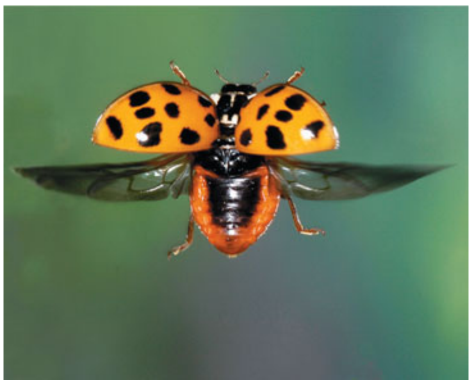
A variety of specialized gas exchange organs have evolved in arthropods. Most aquatic species have gills with thin, feathery extensions that place an extensive surface area in contact with the surrounding water. Terrestrial arthropods generally have internal surfaces specialized for gas exchange. Most insects, for instance, have tracheal systems, branched air ducts leading into the interior from pores in the cuticle. These ducts infiltrate the body, carrying oxygen directly to cells.

Insects

One of the arthropod groups that colonized land, the insects and their relatives, is more species-rich than all other eukaryotic groups combined **(Figure 27.20)**. 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 oldest insect fossils date to about 416 million years ago. Later, an explosion in insect diversity took place when insect flight evolved during the Carboniferous and Permian periods (359–251 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 ground. Many insects have one or two pairs of wings that emerge from the dorsal side of the thorax **(Figure 27.21)**. Because the wings are extensions of the cuticle, insects can fly without sacrificing any walking legs. 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.

Insects also radiated in response to the origin of new plant species, which provided new sources of food. As you read in Chapter 22, 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



◀ **Figure 27.21 Ladybird beetle in flight.**

mid-Cretaceous period (about 90 million years ago). Although insect and plant diversity decreased during the Cretaceous mass extinction, both groups rebounded over the past 65 million years.

Terrestrial Vertebrates

Another key event in the colonization of land by animals took place 365 million years ago, when the fins of a lineage of lobe-fins evolved into the limbs and feet of tetrapods. Until then, all vertebrates had shared the same basic fishlike anatomy. After tetrapods moved onto land, they developed many new forms, from leaping frogs to flying eagles to bipedal humans.

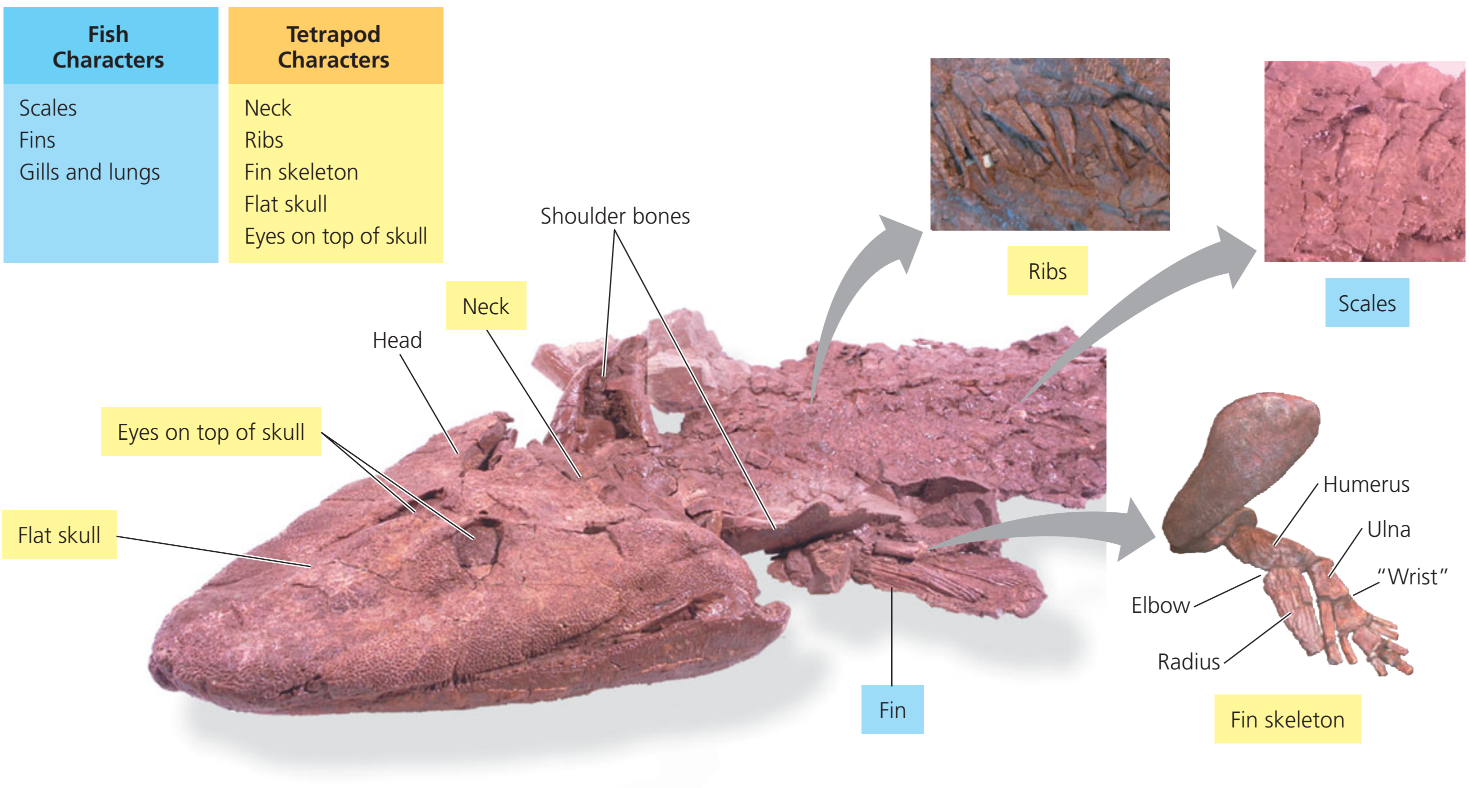
The most significant character of tetrapods gives the group its name, which means "four feet" in Greek. In place of pectoral and pelvic fins, tetrapods have limbs with digits. Limbs support a tetrapod's weight on land, while feet with digits efficiently transmit muscle-generated forces to the ground when the tetrapod walks.

The Origin of Tetrapods

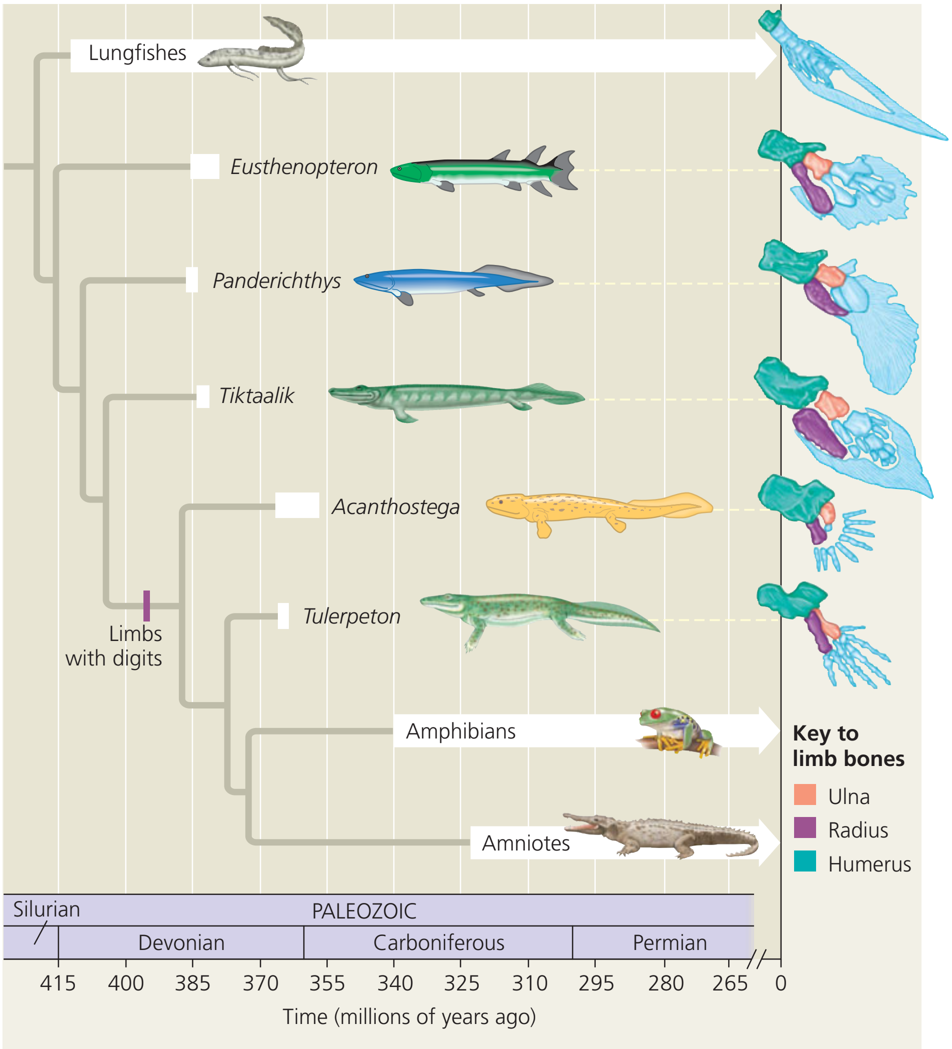
The Devonian coastal wetlands were home to a wide range of lobe-fins. Those that entered shallow, oxygen-poor water could use their lungs to breathe air. Some species probably used their stout fins to help them move across logs or the muddy bottom. Thus, the tetrapod body plan did not evolve "out of nowhere" but was simply a modification of a preexisting body plan.

The discovery in 2006 of a fossil called *Tiktaalik* has provided new details on how this process occurred **(Figure 27.22)**. 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 and shoulders, allowing it to move its head about. Finally, the bones of *Tiktaalik*'s front fin had 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. Although it is unlikely that *Tiktaalik* could walk on land, its front fin skeleton suggests that it could prop itself up in water on its fins.

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 27.23)**. Over the next 60 million years, a great diversity of tetrapods arose. 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 27.22 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.



▲ **Figure 27.23 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.

WHAT IF? *If the most recent common ancestor of* Tulerpeton *and living tetrapods originated 380 million years ago, what range of dates would include the origin of amphibians?*

▲ Salamanders retain their tails as adults.

▲ Caecilians have no legs and are mainly burrowing animals.

◀ Frogs and toads lack tails as adults.

▲ **Figure 27.24 Amphibian diversity.**

Amphibians

The **amphibians** are represented today by about 6,150 species of salamanders, frogs, and caecilians **(Figure 27.24)**. Some salamanders 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 also found in early terrestrial tetrapods.

Frogs are better suited than salamanders for moving on land. 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.

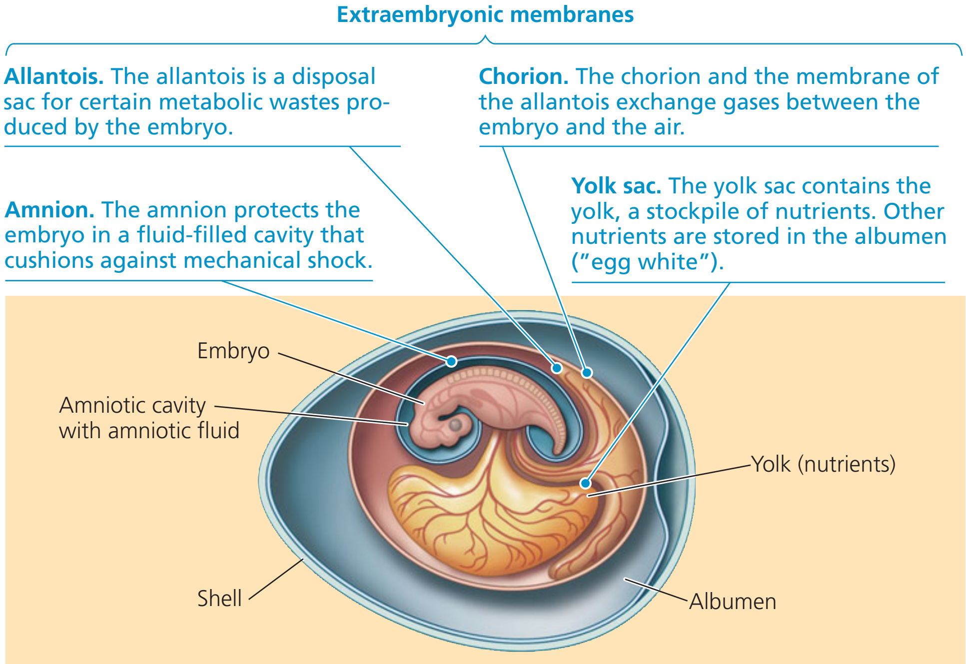
Finally, the caecilians are legless and nearly blind. Their lack of legs is a secondary adaptation, as they evolved from a legged ancestor. Caecilians inhabit tropical areas, where most species burrow in moist forest soil.

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.

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, habitat loss, climate change, and pollution. These and other factors have not only reduced populations, but also led to extinctions.

Terrestrial Adaptations in Amniotes

Compared to the amphibians, a more extensive colonization of dry habitats occurred in the **amniotes**, a group of tetrapods whose extant members are the reptiles (including birds, as we'll discuss shortly) and mammals. 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



▲ **Figure 27.25 The amniotic egg.** The embryos of reptiles and mammals form four extraembryonic membranes: the amnion, chorion, yolk sac, and allantois. This diagram shows these membranes in the shelled egg of a reptile.

allantois **(Figure 27.25)**. The amniotic egg was a key evolutionary innovation for terrestrial life: It allowed the embryo to develop on land in its own private "pond," 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 land plants; see Chapter 26.) Most mammals have dispensed with the eggshell over the course of their evolution, and the embryo avoids desiccation by developing within the amnion inside the mother's body.

The Origin and Radiation of Amniotes

The most recent common ancestor of living amphibians and amniotes lived about 350 million years ago. Based on where their fossils have been found, the earliest amniotes appear to have lived in warm, moist environments, as did the first tetrapods. Over time, however, early amniotes expanded into a wide range of new environments, including dry and high-latitude regions. The earliest amniotes resembled a small lizard with sharp teeth, a sign that they were predators.

Amniotes today include two large clades of terrestrial vertebrates, reptiles and mammals.

Reptiles Living members of the **reptile** clade include tuataras, lizards and snakes, turtles, crocodilians, and birds **(Figure 27.26)**. There are about 18,300 species of reptiles, the majority of which are squamates (lizards and snakes; 7,900 species) or birds (10,000 species). Notice in Figure 27.26 that dinosaurs are reptiles and that birds originated from saurischian dinosaurs (a group that includes *Tyrannosaurus rex*); as a result, birds are also considered reptiles.

Fossils indicate that the earliest reptiles lived about 310 million years ago and resembled lizards. Reptiles have diverged greatly since then, but as a group they share several derived characters. 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. Fertilization must occur 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 extensively to control their body temperature. However, they do regulate their body temperature through behavioral adaptations. For example, many lizards bask in the sun when the air is cool and seek shade when the air is 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. However, the reptile clade is not entirely ectothermic; birds are **endothermic**, capable of maintaining body temperature through metabolic activity.

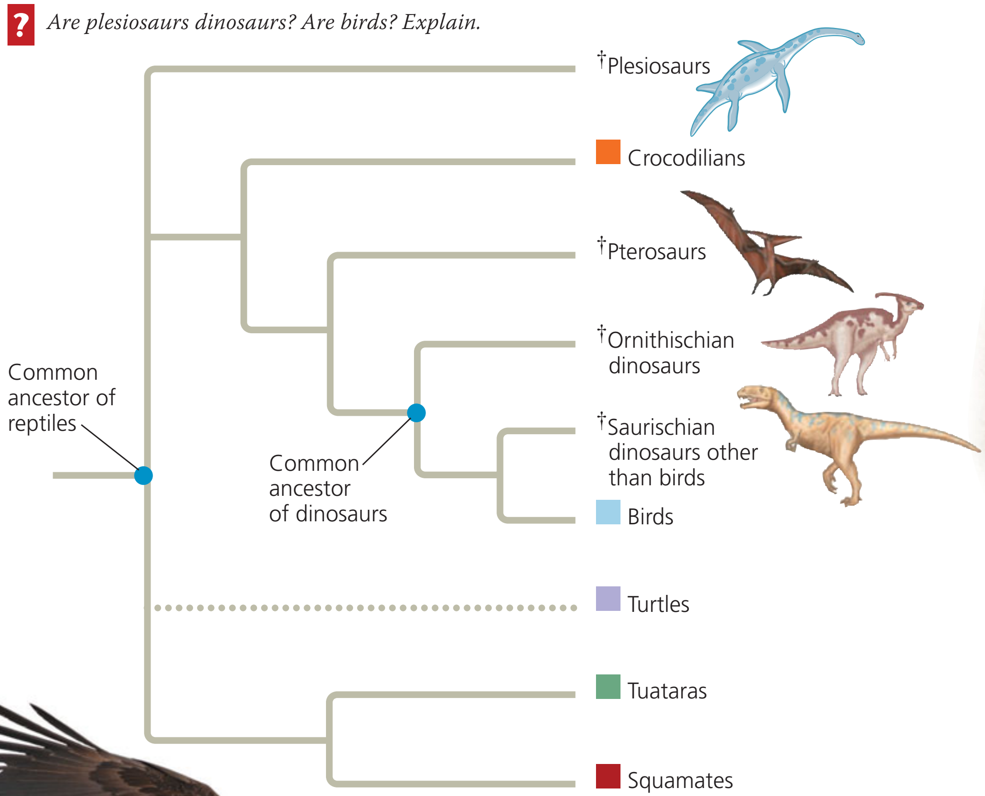
Mammals The reptiles we have been discussing represent one of the two living lineages of amniotes. The other amniote lineage is our own, the **mammals**, named for their distinctive mammary glands, which produce milk for offspring. Hair, another mammalian characteristic, and a fat layer under the skin help the body retain heat. Like birds, mammals are endothermic, and most have a high metabolic rate. In addition, whereas the teeth of reptiles are generally uniform in size and shape, the jaws of mammals 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; see Figure 33.14).

Mammals originated from a group of amniotes called **synapsids**. Early nonmammalian synapsids lacked hair, had a sprawling gait, and laid eggs. Over the course of 120 million years, these ancestors gave rise to a series of increasingly mammal-like synapsids (see Figure 23.4). Finally, about 180 million years ago, the first true mammals arose. A diverse set of mammals coexisted with dinosaurs from 180 to 65 million years ago, but these species were not abundant and most measured less than 1 m. One possible explanation for their small size is that dinosaurs already occupied ecological niches of large-bodied animals.

▼ Figure 27.26 Exploring Reptilian Diversity

The reptile clade consists of five groups with living members, shown below, along with extinct groups such as the plesiosaurs, pterosaurs, and nonflying dinosaurs. The dotted line indicates the uncertain relationship of turtles to other reptiles.

? *Are plesiosaurs dinosaurs? Are birds? Explain.*



Crocodilians. Crocodiles and alligators (23 species, collectively called crocodilians) belong to an ancient lineage whose earliest members lived on land more than 200 million years ago. Later, some species adapted to life in water, breathing air through their upturned nostrils.

Birds. The anatomy of birds (10,000 species) includes many adaptations that facilitate flight, such as the lightweight "honey-combed" structure of their bones and stiff feathers that contribute to the aerodynamic shapes of their wings.

Turtles. The 307 species in this group have a boxlike shell fused to their skeletons. Some turtles live on land, while others live in freshwater or marine habitats, but all are air-breathing.

Tuataras. Although their ancestors were widespread during the Cretaceous period, today the two living species of tuataras are found only on 30 islands off the coast of New Zealand.

Squamates. Snakes, together with lizards, make up the squamate lineage of reptiles (7,910 species). Snakes are carnivorous, and despite their lack of legs, have adaptations that make them effective predators, including the ability of various species to detect heat, chemicals, or vibrations that signal the presence of prey.

▼ **Figure 27.27 The major mammalian lineages.**

Monotremes

Found only in Australia and New Guinea, there are five extant species of monotremes (the platypus and four species of spiny anteaters). Monotremes have hair and produce milk, but they lack nipples. They are the only mammals that lay eggs (inset).

Marsupials

Kangaroos, opossums, and koalas are examples of marsupials (324 species). Like eutherians, they have nipples that provide milk and they give birth to live young. Offspring are born early in development; they finish their growth while nursing from a nipple (in their mother's pouch in most species).

Eutherians

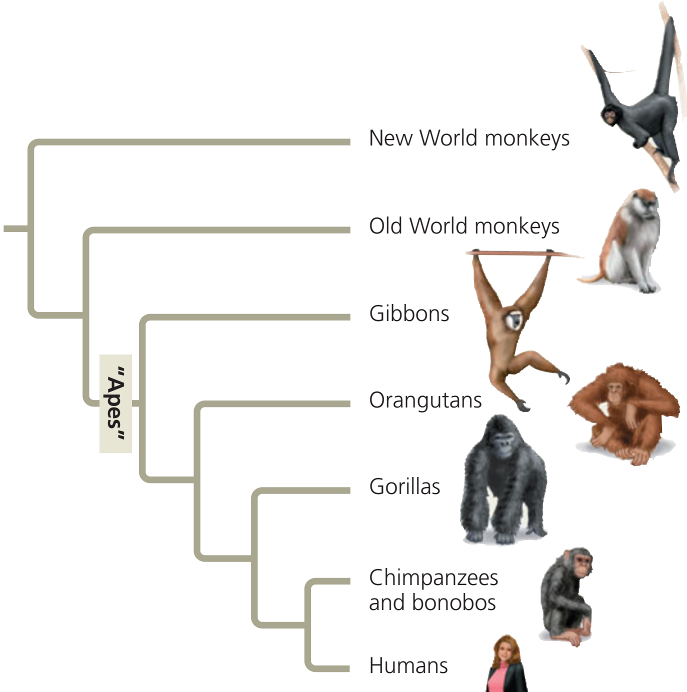
Most mammals are eutherians, a clade that include primates, whales, rodents, and many other mammal groups (5,010 species). Eutherians have a longer pregnancy than marsupials, and they have a more complex **placenta** (a structure in which nutrients diffuse into the embryo from the mother's blood).

? *Monotremes are basal mammals. Draw a phylogenetic tree showing evolutionary relationships among the three lineages.*

By 140 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) **(Figure 27.27)**. After the extinction of terrestrial dinosaurs (65 million years ago), mammals continued to diversify, ultimately resulting in the more than 5,300 species living today.

Human Evolution

Humans (*Homo sapiens*) are primates, nested with a group informally called apes **(Figure 27.28)**. Unlike other apes, humans stand upright and are bipedal (walk on two legs). Humans



▲ **Figure 27.28 The human evolutionary tree.** The fossil record shows that monkeys and apes began diverging from other primates about 50 million years ago. The lineages leading to humans branched off from other apes between 6 and 7 million years ago.

also have a larger brain and are capable of language, symbolic thought, artistic expression, and the use of complex tools.

Early human ancestors were bipedal long before their brains increased in size. Consider the 4.4-million-year-old *Ardipithecus ramidus*. This species showed signs of bipedalism, yet its brain (325 cm^3 in volume) was much smaller than that of *H. sapiens* (1,300 cm^3). By 2.5 million years ago, fossils show that human ancestors walked upright and used tools—yet they still had a brain the size of a softball.

The earliest fossils placed in our genus, *Homo,* include those of *Homo habilis,* which lived 2.4 to 1.6 million years ago. Compared to earlier human ancestors, *H. habilis* had a shorter jaw and a larger brain volume, about 675 cm^3. Brain size, body size, and tool use continued to increase over time in various fossil *Homo* species, some of which lived as recently as 28,000 years ago. Our own species, *H. sapiens,* appears to have originated in Africa about 200,000 years ago and spread from there around the world **(Figure 27.29)**.

▲ **Figure 27.29 Early fossils of *Homo sapiens*.** These fossilized remains of an adult and a child, discovered in a cave in Israel, are thought to be around 92,000 years old.

We turn now to the ecological and evolutionary effects of animals—including humans.

CONCEPT CHECK 27.4

1. Describe two adaptations that have enabled insects to thrive on land.
2. **MAKE CONNECTIONS** Compare and contrast how the colonization of land by plants and by vertebrates exemplifies descent with modification. (Review Concepts 19.2 and 26.1.)
3. **WHAT IF?** Which came first, the chicken or the egg? Explain, basing your answer on evolutionary principles.

For suggested answers, see Appendix A.

CONCEPT 27.5

Animals have transformed ecosystems and altered the course of evolution

The rise of animals coincided with one of the most monumental changes in the history of life: the transformation of a microbe-only world to a world filled with large producers, predators, and prey. This change affected all aspects of ecological communities, in the sea and on land.

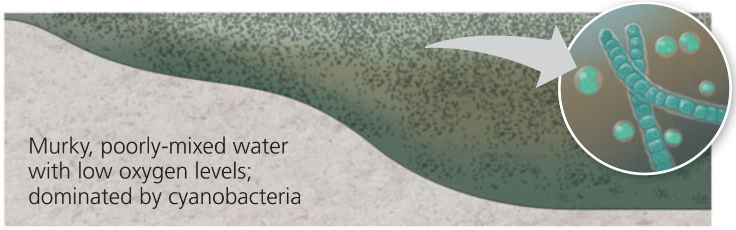
Ecological Effects of Animals

As we saw in Chapter 25, until 600 million years ago, life in the oceans was almost entirely microscopic. Among other differences from life today, there were no large filter feeders in early marine communities. As a result, researchers think that ocean waters were cloudy, thick with microorganisms and suspended organic matter **(Figure 27.30a)**. Geologic and fossil evidence suggests that these turbid waters also had low oxygen levels and were dominated by cyanobacteria. Marine ecosystems remained in this condition for over a billion years, despite the fact that algae and a variety of heterotrophic eukaryotes were present for most of that time. What changes did the rise of animals bring?

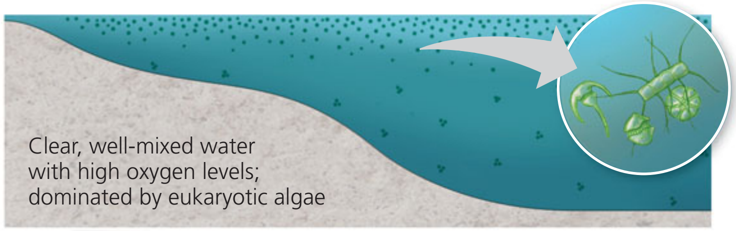
Marine Ecosystems

Fossil biochemical evidence suggests that the abundance of cyanobacteria decreased in the early Cambrian. This decrease may have been caused by the activities of crustaceans and other animals with filter-feeding mouthparts. Such filter feeders can process an enormous amount of water: Every 20 days, animals filter an estimated volume of ocean water equal to that in which most organisms live (the top 500 m). As early filter-feeding animals removed cyanobacteria and other suspended matter from the water, the ocean waters would have become clearer. As a result, algae, which require more light for photosynthesis than do cyanobacteria, increased in abundance and moved to deeper waters **(Figure 27.30b)**.

Along with changes in water clarity and a shift to algae as the dominant producers, a different set of feeding relationships also emerged. A host of small animals evolved that ate marine producers and detritus. Those small animals, in turn, were eaten by larger animals—which were themselves eaten by still larger animals. Overall, the explosion of animal diversity in the early Cambrian marked the end of the microbial world and the beginning of ocean life as we know it today—a world filled with predators, filter feeders, and scavengers of all shapes and sizes.



(a) Ocean conditions before 600 mya



(b) Changes to ocean conditions by 530 mya

▲ **Figure 27.30 A sea change for Earth's oceans.**

Terrestrial Ecosystems

Before animals joined plants and fungi onshore, terrestrial ecosystems had a simple structure: Producers (early land plants) harnessed energy from the sun and drew essential nutrients from the soil, while decomposers returned nutrients to the soil. By 410 million years ago, animals had transformed these ecosystems. Plants and decomposers continued to be important, of course, but new biotic interactions were also in place: Plants were being consumed by herbivorous animals, and they, in turn, were being eaten by predators. Still other animals (detritivores) consumed organic debris, making for a complex network of ecological interactions—much of it driven by animals.

The lesser snow goose (*Chen caerulescens*), a migratory bird that breeds in marsh lands bordering Canada's Hudson Bay, illustrates the impact of animals on terrestrial communities. These birds feed on grasses and other marsh plants. At low population numbers, lesser snow geese improve the growth of marsh plants. This positive effect may be due to the fact that the birds defecate every few minutes as they feed, thereby adding nitrogen (which plants need to grow) to the soil. At high population numbers, however, the feeding activities of the birds can destroy a marsh, converting it to a mudflat **(Figure 27.31)**.

▶ **Figure 27.31 Effects of herbivory.** The area inside the fence, which the geese could not access, shows the original state of the marsh.

Evolutionary Effects of Animals

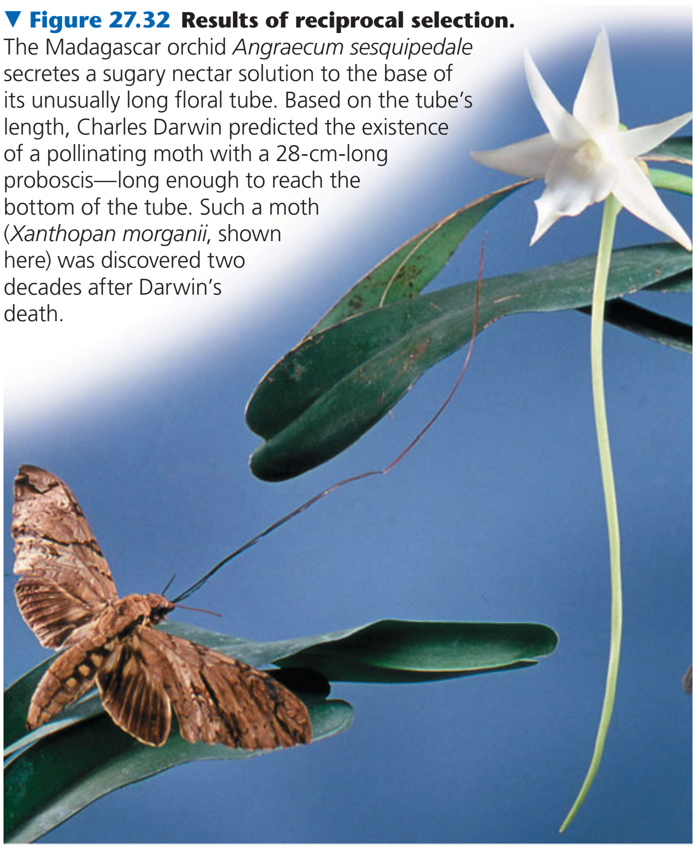
The rise of animals also set in motion a series of profound evolutionary changes. As we've seen, many of these changes resulted from the fact that animals can make life dangerous: The origin of mobile, heterotrophic animals with a complete digestive tract drove some species to extinction and initiated ongoing "arms races" between bilaterian predators and prey.

In this section, we'll consider the related topic of whether increases in animal diversity have led to other evolutionary radiations. Then we'll examine the ongoing evolutionary effects of one particular animal species—humans.

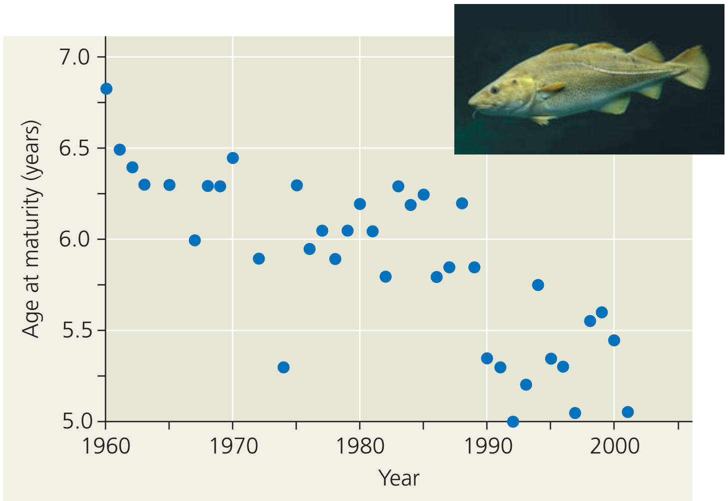
Evolutionary Radiations

Two species that interact can exert selective pressures on one another. A plant (or any other species) that interacts with an animal may evolve in response to selection imposed by the animal—and the animal, in turn, may evolve in response to evolutionary changes in the plant **(Figure 27.32)**. In the **Scientific Skills Exercise**, you can interpret data from a study of selection occurring in a predator-prey interaction over time. Such reciprocal selective pressures also occur when the origin of new species in one group of organisms stimulates further radiations in other organisms, especially those that can eat, escape from, or compete effectively with the new group.

As animal groups have diversified, they have often had this effect. For example, the origin of a new group of animals provides new sources of food for *parasites*, organisms that feed on the tissues of another organism (the *host*). Many parasites feed on a single host species. As a result, the ongoing diversification of animals has led to evolutionary radiations in many groups of parasites—the animals, fungi, protists, and bacteria that can feed on newly evolved animal hosts.



▼ **Figure 27.32 Results of reciprocal selection.** The Madagascar orchid *Angraecum sesquipedale* secretes a sugary nectar solution to the base of its unusually long floral tube. Based on the tube's length, Charles Darwin predicted the existence of a pollinating moth with a 28-cm-long proboscis—long enough to reach the bottom of the tube. Such a moth (*Xanthopan morganii*, shown here) was discovered two decades after Darwin's death.



▲ **Figure 27.33 Reproducing at a younger age.** Age at sexual maturity has dropped over time in heavily fished populations of northern cod (*Gadus morhua*). Size at maturity has also dropped (not shown).

? *Fish that reproduce when they are younger and smaller typically have fewer offspring than fish that reproduce when they are older and larger. Predict how evolution in response to fishing will affect the ability of cod populations to recover from overfishing.*

Human Impacts on Evolution

As can be seen from satellite photographs or the window of an airplane, humans have dramatically altered the environment. By making large changes to the environment, we have altered the selective pressures faced by many species. This suggests that we are likely causing evolutionary change—and we are. For example, by using antibiotics to kill bacteria, we have (inadvertently) caused the evolution of resistance in bacterial populations (see Concept 19.3). We have also caused evolutionary change in species that we hunt for sport or food. For example, in cod and other fishes harvested for food, commercial fisheries target older and larger fish. This has led to a reduction in the age and size at which individuals reach sexual maturity **(Figure 27.33)**. Natural selection has favored fish that mature at a younger age and smaller size because such individuals are more likely to reproduce before they are caught than are individuals that mature when they are older and larger.

In addition to causing evolution by natural selection, our actions may cause a mass extinction, thereby greatly altering the future course of evolution. Species extinction rates have increased greatly in the last 400 years, raising concern that unless dramatic preventative measures are taken, a sixth, human-caused mass extinction may occur (see Chapter 23). Among the many taxa under threat, molluscs have the dubious distinction of being the animal group with the

Scientific Skills Exercise

Understanding Experimental Design and Interpreting Data

Is There Evidence of Selection for Defensive Adaptations in Mollusc Populations Exposed to Predators? The course of animal evolution has been shaped by the interactions of predator and prey species. The fossil record provides evidence that historically, increased risk to prey species from predators is often accompanied by increased incidence and expression of prey defenses.

A team of researchers studied the possible selective pressure exerted by a predator, the European green crab (*Carcinus maenas*), on its prey, the flat periwinkle (*Littorina obtusata*), a mollusc, in the Gulf of Maine. Periwinkles from southern sites in the Gulf 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.

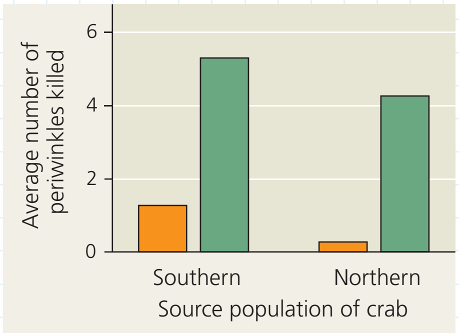
Previous research shows that (1) flat periwinkle shells recently collected from the Gulf are thicker than those collected in the late 1800s, and (2) periwinkle populations from southern sites in the Gulf have thicker shells than periwinkle populations from northern sites. In this exercise, you'll interpret the design and results of the researchers' experiment studying the rates of predation by European green 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



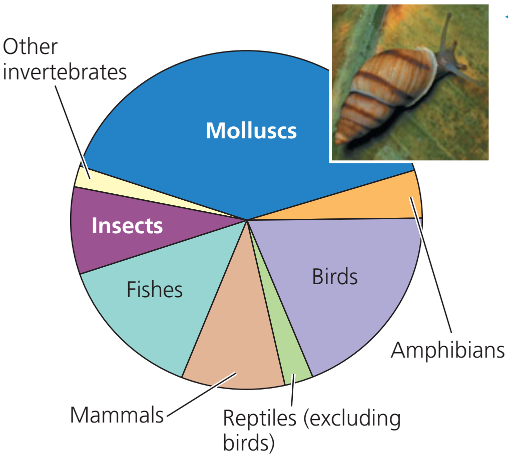
When the researchers presented the crabs with unshelled periwinkles, all the unshelled periwinkles were consumed in less than an hour.

Interpret the Data

1. What hypothesis were the researchers testing in this study? What are the independent variables in this study? What are the dependent variables in this study?
2. Why did the research team set up four different treatments?
3. Why did researchers present unshelled periwinkles to the crabs? Explain the significance of the results of this part of the experiment.
4. Summarize the results of the experiment in words. 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.

Data from R. Rochette, S. P. Doyle, and T. C. Edgell, Interaction between an invasive decapod and a native gastropod: Predator foraging tactics and prey architectural defenses, *Marine Ecology Progress Series* 330:179–188 (2007).

MB A version of this Scientific Skills Exercise can be assigned in MasteringBiology.



▲ Recorded extinctions of animal species

◀ An endangered Pacific island land snail, *Partula suturalis*

▲ Workers on a mound of pearl mussels killed to make buttons (ca. 1919)

▲ **Figure 27.34 The silent extinction.** Molluscs account for a largely unheralded but sobering 40% of all documented extinctions of animal species. These extinctions have resulted from habitat loss, pollution, introduced species, overharvesting, and other human actions. 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 such as the species pictured above are highly vulnerable to the same threats; like pearl mussels, they are among the world's most imperiled animal groups.

largest number of documented extinctions **(Figure 27.34)**. Pearl mussels, a group of freshwater molluscs that can make natural pearls, are among the world's most endangered animals. Thirty of the pearl mussel species that once lived in North America have become extinct in the last 100 years, and nearly 200 of the 270 that remain are threatened by extinction.

Threats faced by pearl mussels and other molluscs include habitat loss, pollution, and competition or predation by non-native species introduced by people. 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 species can be revived.

Our discussion of how humans affect evolution brings this unit on the history of life to an end. But this organization isn't meant to imply that life consists of a ladder leading from lowly microorganisms to lofty humanity. The history of life shows that biological diversity is the product of branching phylogeny, not ladderlike "progress," however we choose to measure it. The fact that there are almost as many species of ray-finned fishes alive today as in all other vertebrate groups combined is a clear indication that our finned relatives are not outmoded underachievers that failed to leave the water. 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 27.5

1. Describe how ocean communities changed in the early Cambrian period, and explain how animals may have influenced those changes.
2. How did the colonization of land by animals affect terrestrial communities?
3. **MAKE CONNECTIONS** Human actions often break large areas of forest or grassland into small remnant parcels that support fewer individuals and are far apart from one another. Predict how gene flow, genetic drift, and extinction risk would differ between the original and the remnant populations. (Review Concept 21.3.)

For suggested answers, see Appendix A.

27 Chapter Review

SUMMARY OF KEY CONCEPTS

CONCEPT 27.1

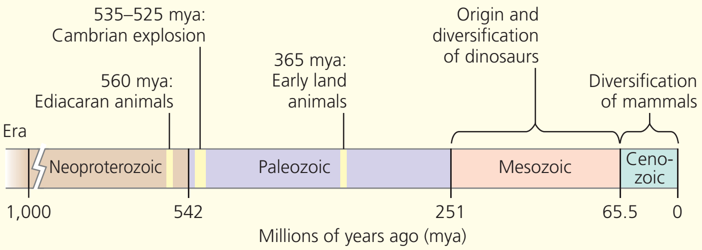
Animals originated more than 700 million years ago (pp. 528–530)

- The earliest evidence of animal life comes from fossil steroids indicative of sponges that date to 710 million years ago.
- The first fossils of large animals date to 560 million years ago and include sponges as well as fossil organisms that resemble living cnidarians and molluscs.
- Sponges are basal animals that, unlike nearly all other animals, lack true tissues. Cnidarians are one of the oldest lineages of **eumetazoans**, an animal clade whose members have tissues.

? *What features are shared by sponges and choanoflagellates? Interpret these observations.*

CONCEPT 27.2

The diversity of large animals increased dramatically during the "Cambrian explosion" (pp. 530–532)



- Prior to the **Cambrian explosion** (535–525 million years ago), virtually all large animals were soft-bodied and poorly defended.
- Fossils dating to the Cambrian explosion include the oldest known members of many living animal phyla, some of which had features for capturing prey while others had defensive adaptations such as spines and body armor.
- Fossil and molecular evidence suggests that **bilaterians** had emerged by 635 million years ago.

? *What caused the Cambrian explosion? Describe current hypotheses.*

CONCEPT 27.3

Diverse animal groups radiated in aquatic environments (pp. 532–539)

- The diverse animals that emerged from the Cambrian explosion can be categorized by their **body plan**, the morphological and developmental traits that are integrated into a functional whole, the living animal.
- Most living animals are bilaterians, bilaterally symmetric animals with three tissue layers and a complete digestive tract.
- Bilaterally symmetric animals have diverged into three major clades: Lophotrochozoa, Ecdysozoa, and Deuterostomia.
- By 420 million years ago, aquatic bilaterians had radiated into a diverse set of **invertebrate** clades, along with three major clades of **vertebrates**: chondrichthyans, ray-finned fishes, and lobe-fins.

? **DRAW IT** *Draw a phylogenetic tree showing relationships among Lophotrochozoa, Cnidaria, Ecdysozoa, Ctenophora, Porifera, and Deuterostomia. On the tree, mark the animal common ancestor as well as the origin of three germ layers, true tissues, and bilateral symmetry.*

CONCEPT 27.4

Several animal groups had features facilitating their colonization of land (pp. 539–547)

- Unlike plants, whose ancestors colonized land only once, many animal groups have made the transition to terrestrial life.
- Animals that colonized land were "pre-adapted" for their new environment in that they already had a complete digestive tract and well-developed skeletal, muscle, and nervous systems.
- Arthropods were the first animals to colonize land, about 450 million years ago. Among the arthropods that colonized land, the insects radiated explosively and now contain more known species than all other eukaryotic groups combined.
- Vertebrates colonized land 365 million years ago when early tetrapods arose from aquatic lobe-fins. Amphibians, an early-diverging group of tetrapods, are more dependent on water than are amniotes, a diverse group whose living members include reptiles and mammals.

? *Describe the amniotic egg and evaluate its significance.*

CONCEPT 27.5

Animals have transformed ecosystems and altered the course of evolution (pp. 547–550)

- The rise of animals coincided with the change from a microbe-only world to a world filled with large producers, scavengers, predators, and prey.
- The origin of animals with filter-feeding mouthparts may have caused sweeping changes in early oceans, such as an increase in water clarity and a shift from cyanobacteria to algae as the dominant producers.
- The diversification of bilaterians in the sea and on land has changed biotic interactions and stimulated evolutionary radiations in other groups of organisms.
- Human actions have caused evolution by natural selection and have the potential to cause a mass extinction.

? *Explain how the activities of animals (including humans) can lead to evolutionary change, and provide an example.*

TEST YOUR UNDERSTANDING

Level 1: Knowledge/Comprehension

1. Which of the following clades contains the greatest number of animal species?
a. the vertebrates
b. the bilaterians
c. the sponges
d. the deuterostomes
e. the insects

2. Fossil steroid and molecular clock evidence suggests that animals originated
a. between 770 and 710 million years ago.
b. more than 100 million years before the oldest known fossils of large animals.
c. during the Cambrian explosion.
d. after sponges diverged from other metazoans.
e. both a and b

3. Which of the following was probably the *least* important factor in bringing about the Cambrian explosion?
a. the emergence of predator-prey relationships among animals
b. the accumulation of diverse adaptations, such as shells and different modes of locomotion
c. the origin of *Hox* genes and other genetic changes affecting the regulation of developmental genes
d. the movement of animals onto land
e. the accumulation of sufficient atmospheric oxygen to support the more active metabolism of mobile animals

4. 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 gnathostome 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
e. an early terrestrial caecilian whose legless condition had evolved secondarily

Level 2: Application/Analysis

5. Which clade does *not* include humans?
a. synapsids
b. lobe-fins
c. lophotrochozoans
d. tetrapods
e. osteichthyans

6. In Figure 27.10, the Deuterostomia clade is most closely related to which two main clades?
a. Ctenophora and Cnidaria
b. Lophotrochozoa and Ecdysozoa
c. Cnidaria and Bilateria
d. Platyhelminthes and Rotifera
e. Echinodermata and Hemichordata

Level 3: Synthesis/Evaluation

7. **SCIENTIFIC INQUIRY**

DRAW IT As a consequence of size alone, organisms that are large tend to have larger brains than organisms that are small. However, some organisms have brains that are considerably larger than expected for an animal of their size. There are high energy 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 ancestors of humans. In such lineages, what can you infer about the relative 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

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.

8. **FOCUS ON EVOLUTION**
In Figure 27.26, circle the monophyletic group that includes dinosaurs. Explain your answer and list the taxa that are in this clade. Knowing that birds are endothermic and crocodiles are ectothermic, can phylogenetic bracketing be used to predict whether dinosaurs other than birds are ectothermic or endothermic?

9. **FOCUS ON 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 in biological communities.

For selected answers, see Appendix A.