

Retroviruses. **Retroviruses** [*L. retro*, backward, and *virus*, poison] are RNA animal viruses that have a DNA stage. Figure 20.4 illustrates the reproduction of a retrovirus—namely, HIV (human immunodeficiency virus), the cause of AIDS. A retrovirus contains a special enzyme called **reverse transcriptase**, which carries out RNA \rightarrow DNA transcription. First, the enzyme synthesizes a DNA strand called cDNA because it is complementary to viral RNA, and then the enzyme uses cDNA as a template to form double-stranded DNA. Using host enzymes, double-stranded DNA is integrated into the host genome. The viral DNA remains in the host genome and is replicated when host DNA is replicated. When and if this DNA is transcribed, new viruses are produced by the steps we have already cited: biosynthesis, maturation, and release; in this instance, by plasma membrane budding.

Viral Infections of Special Concern

All viral infections of humans and other organisms are challenging to treat, especially because antibiotics designed to interfere with bacterial metabolism have no effect on viral illnesses. By learning how viruses replicate in cells, scientists have been able to design drugs to help treat certain viral infections. For example, the reverse transcriptase inhibitor AZT is used to block the replication of HIV. Acyclovir, a drug used to treat herpes, inhibits the replication of viral DNA. Certain viral infections are especially serious because they lead to even more severe diseases. In humans, papillomaviruses, herpesviruses, hepatitis viruses, adenoviruses, and retroviruses are associated with specific types of cancer. Emerging viruses are of recent concern.

Emerging Viruses

Some emerging diseases—new or previously uncommon illnesses—are caused by viruses that are now able to infect large numbers of humans. These viruses are known as **emerging viruses**. Examples of emerging viral diseases are AIDS, West Nile encephalitis, hantavirus pulmonary syndrome (HPS), severe acute respiratory syndrome (SARS), Ebola hemorrhagic fever, and avian influenza (bird flu).

Several different types of events can cause a viral disease to suddenly “emerge” and start causing a widespread human illness. A virus can extend its range when it is transported from one part of the world to another. West Nile encephalitis is a virus that extended its range after being transported into the United States, where it took hold in bird and mosquito populations. SARS was transported from Southeast Asia to Toronto, Canada.

Viruses are well known for their high mutation rates. Sometimes viruses that formerly infected animals other than humans can “jump” species and start infecting humans due to a change in their capsids or spikes that enables them to attach to human cell receptors, as discussed in the Health Focus on page 360.

Viroids and Prions

At least a thousand different viruses cause diseases in plants. About a dozen diseases of crops, including potatoes, coconuts, and citrus, have been attributed not to viruses but to **viroids**, which are naked strands of RNA (not covered by a capsid). Like viruses, though, viroids direct the cell to produce more viroids.

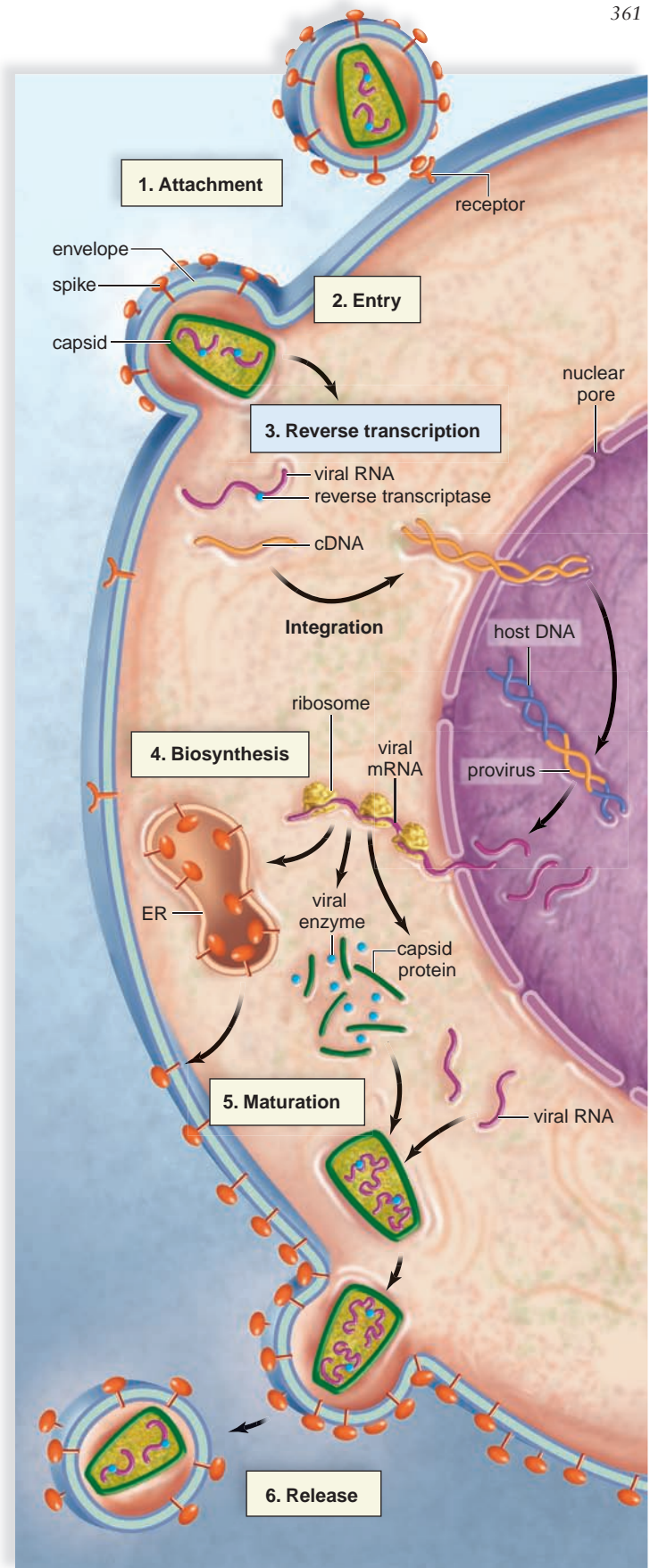


FIGURE 20.4 Reproduction of the retrovirus HIV.

HIV uses reverse transcription to produce a DNA copy (cDNA) of RNA genes; double-stranded DNA integrates into the cell's chromosomes before the virus reproduces and buds from the cell. The steps in color are unique to retroviruses.

A number of fatal brain diseases, known as TSEs,¹ have been attributed to **prions**, a term coined for *proteinaceous infectious* particles. The discovery of prions began when it was observed that members of a primitive tribe in the highlands of Papua New Guinea died from a disease commonly called kuru (meaning trembling with fear) after participating in the cannibalistic practice of eating a deceased person's brain. The causative agent was smaller than a virus—it was a misshapen protein. The normal prion protein is found in healthy brains, although its function is unknown. It appears that TSEs result when a normal prion protein changes shape so that the polypeptide chain is in a different configuration. It is hypothesized that a misshapen prion can interact with a normal prion protein to change its shape, but the mechanism is unclear.

Check Your Progress

20.1

1. What are the two components shared by all viruses?
2. Viruses are generally considered to be nonliving. Should viroids and prions also be viewed as nonliving? Why or why not?
3. From an evolutionary standpoint, why is it beneficial to a virus if its host lives and does not die?

¹TSEs (transmissible spongiform encephalopathies)

20.2 The Prokaryotes

As previously mentioned, the **prokaryotes** include bacteria and archaea, which are fully functioning cells. Because they are microscopic, the prokaryotes were not discovered until the Dutch microscopist Antonie van Leeuwenhoek (1632–1723), better known as the father of the microscope, first described them along with many other microorganisms. Leeuwenhoek and others after him believed that the “little animals” that he observed could arise spontaneously from inanimate matter. For about 200 years, scientists carried out various experiments to determine the origin of microorganisms in laboratory cultures. Finally, in about 1850, Louis Pasteur devised an experiment for the French Academy of Sciences that is described in Figure 20.5. It showed that a previously sterilized broth cannot become cloudy with growth unless it is exposed directly to the air, where bacteria are abundant. Today we know that bacteria are plentiful in air, water, and soil and on most objects. In the pages following, the general characteristics of prokaryotes are discussed before those specific to the bacteria (domain Bacteria) and then the archaea (domain Archaea) are considered in more detail.

Structure of Prokaryotes

Prokaryotes generally range in size from 1 to 10 μm in length and from 0.7 to 1.5 μm in width. The term *prokaryote* means “before a nucleus,” and these organisms lack a eukaryotic

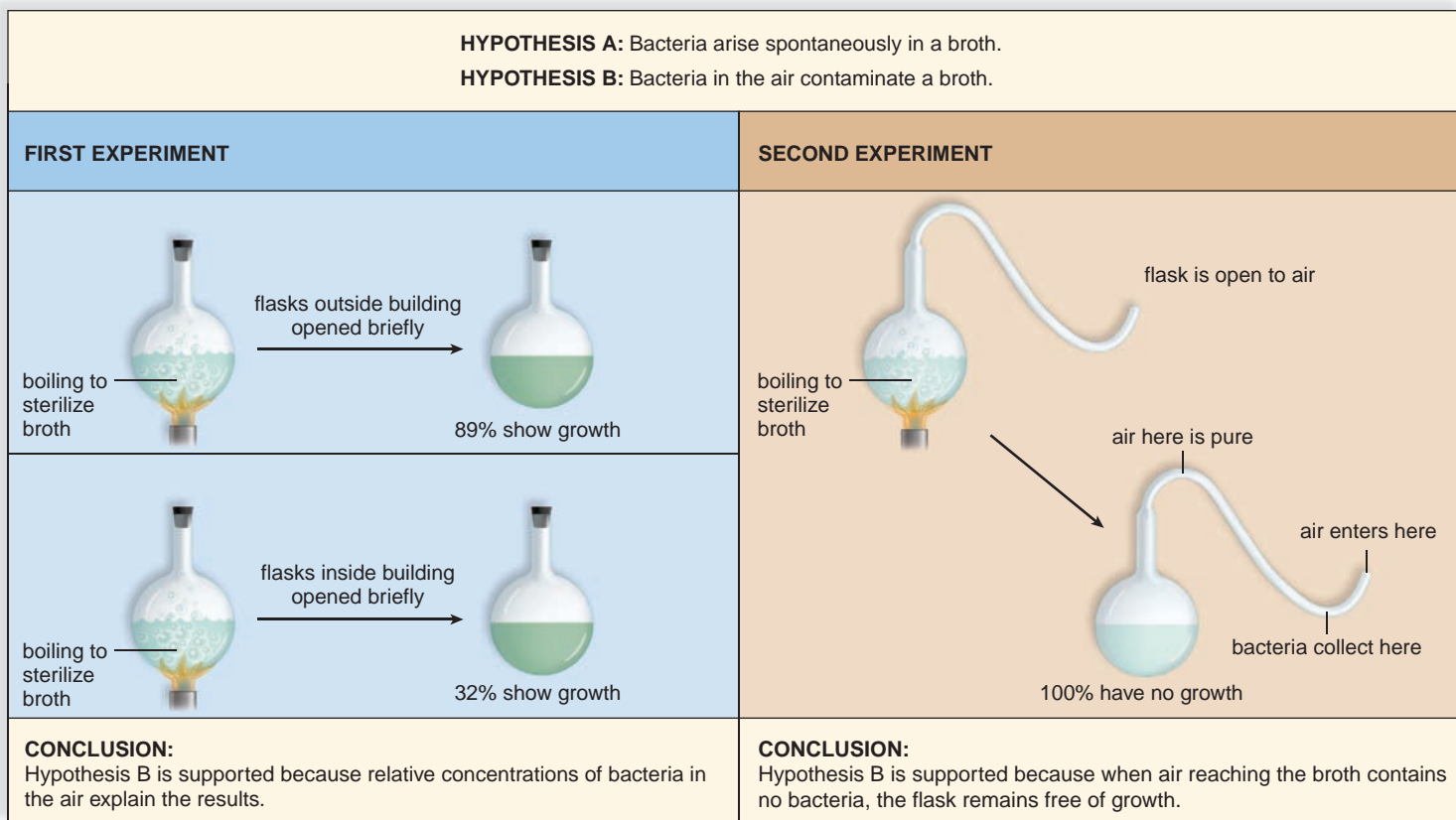


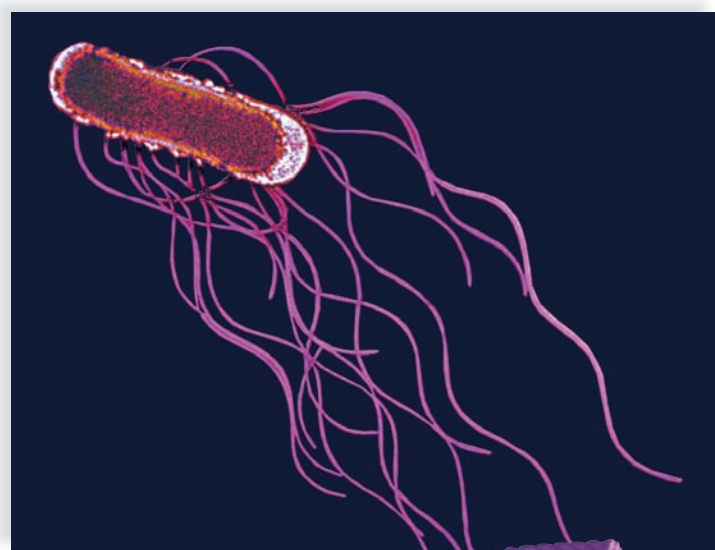
FIGURE 20.5 Pasteur's experiment.

Pasteur disproved the theory of spontaneous generation of microbes by performing these types of experiments.

nucleus. There are prokaryotic fossils dated as long ago as 3.5 billion years, and the fossil record indicates that the prokaryotes were alone on Earth for at least 1.3 billion years. During that time, they became extremely diverse in structure and especially diverse in metabolic capabilities. Prokaryotes are adapted to living in most environments because the various types differ in the ways they acquire and use energy.

A typical prokaryotic cell has a cell wall situated outside the plasma membrane. The cell wall prevents a prokaryote from bursting or collapsing due to osmotic changes. Yet another layer may exist outside the cell wall. The structure and composition of this layer vary among the different kinds of prokaryotes. In many bacteria, the cell wall is surrounded by a layer of polysaccharides called a glycocalyx. A well-organized glycocalyx is called a capsule, while a loosely organized one is called a slime layer. Many bacteria and archaea have a layer comprised of protein, or glycoprotein, instead of a glycocalyx; such a layer is called an S-layer. In parasitic forms of bacteria, these outer coverings help protect the cell from host defenses.

Some prokaryotes move by means of **flagella** (Fig. 20.6). A bacterial flagellum has a filament composed of strands of the protein flagellin wound in a helix. The filament is inserted into a hook that is anchored



TEM 13,250×

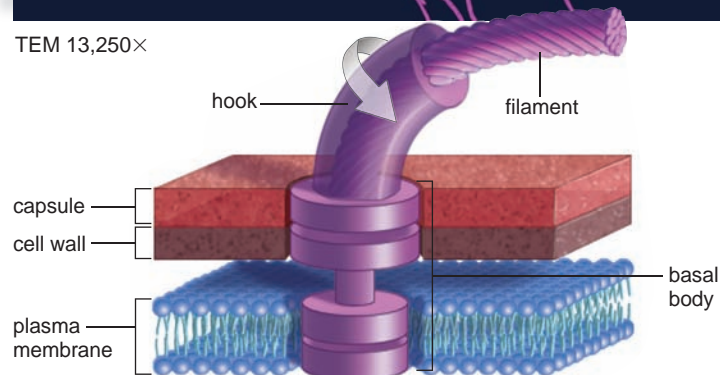


FIGURE 20.6 Flagella.

Each flagellum of a bacterium contains a basal body, a hook, and a filament. The arrow indicates that the basal body, hook, and filament turn 360°. The flagellum of an archaeon is more slender and may lack a basal body.

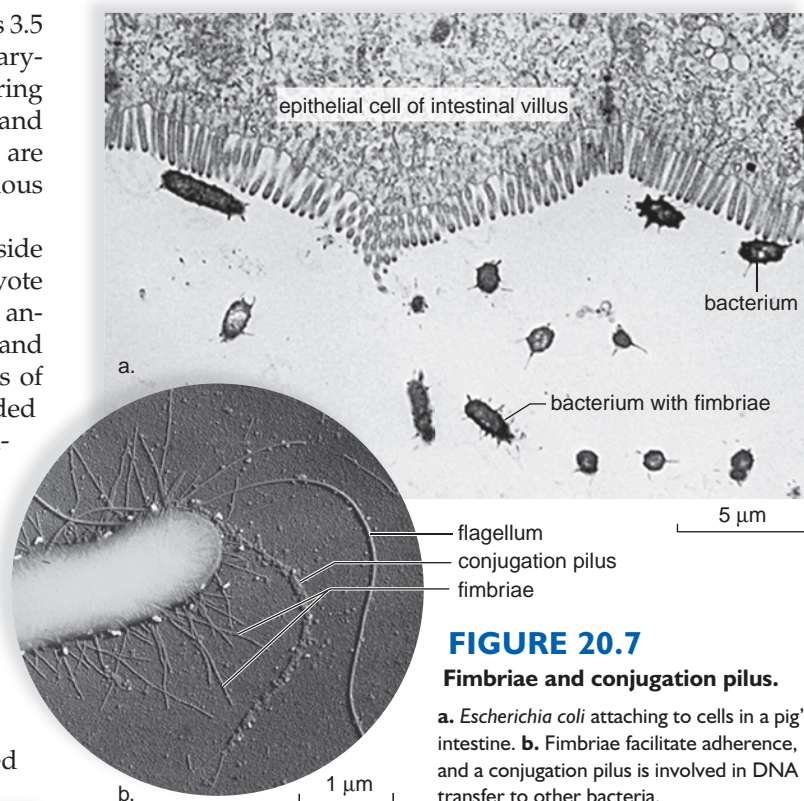


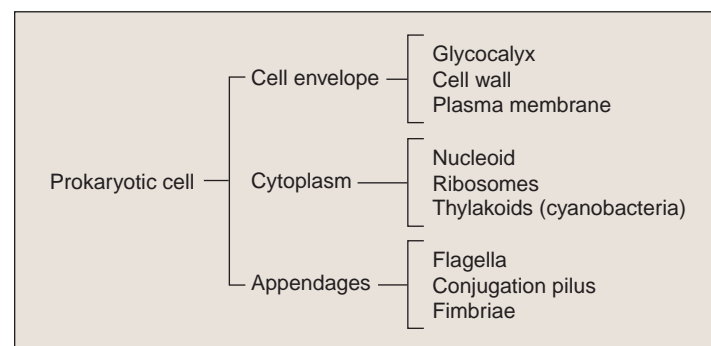
FIGURE 20.7

Fimbriae and conjugation pilus.

a. *Escherichia coli* attaching to cells in a pig's intestine. **b.** Fimbriae facilitate adherence, and a conjugation pilus is involved in DNA transfer to other bacteria.

by a basal body. The 360° rotation of the flagellum causes the cell to spin and move forward. The archaeal flagellum is similar, but more slender and apparently lacking a basal body. Many prokaryotes adhere to surfaces by means of **fimbriae**, short bristlelike fibers extending from the surface (Fig. 20.7). The fimbriae of the bacterium *Neisseria gonorrhoeae* allow it to attach to host cells and cause gonorrhea.

A prokaryotic cell lacks the membranous organelles of a eukaryotic cell, and various metabolic pathways are located on the inside of the plasma membrane. Although prokaryotes do not have a nucleus, they do have a dense area called a **nucleoid** where a single chromosome consisting largely of a circular strand of DNA is found. Many prokaryotes also have accessory rings of DNA called **plasmids**. Plasmids can be extracted and used as vectors to carry foreign DNA into host bacteria during genetic engineering processes. Protein synthesis in a prokaryotic cell is carried out by thousands of ribosomes, which are smaller than eukaryotic ribosomes. The following diagram summarizes prokaryotic cell structure, which is depicted in Figure 4.4:



Reproduction in Prokaryotes

Mitosis, which requires the formation of a spindle apparatus, does not occur in prokaryotes. Instead, prokaryotes reproduce asexually by means of **binary fission** [L. *binarius*, of two, and *fissura*, cleft, break] (Fig. 20.8).

The single circular chromosome replicates, and then two copies separate as the cell enlarges. Newly formed plasma membrane and cell wall separate the cell into two cells. Prokaryotes have a generation time as short as 12 minutes under favorable conditions. Mutations are generated and passed on to offspring more quickly than in eukaryotes. Also, prokaryotes are haploid, and so mutations are immediately subjected to natural selection, which determines any possible adaptive benefit.

In eukaryotes, genetic recombination occurs as a result of sexual reproduction. Sexual reproduction does not occur among prokaryotes, but three means of genetic recombination have been observed in prokaryotes. During **conjugation**, two bacteria are temporarily linked together, often by means of a **conjugation pilus** (see Fig. 20.7b). While they are linked, the donor cell passes DNA to a recipient cell. **Transformation** occurs when a cell picks up (from the surroundings) free pieces of DNA secreted by live prokaryotes or released by dead prokaryotes. During **transduction**, bacteriophages carry portions of DNA from one bacterial cell to another. Viruses have also been found to infect archaeal cells, and so transduction may play an important role in gene transfer for both domains of prokaryotes.

Check Your Progress

20.2

1. How is a prokaryotic cell structurally different from a eukaryotic cell?
2. Where is the cell wall located relative to the plasma membrane in a typical prokaryotic cell?
3. How is conjugation different from sexual reproduction?

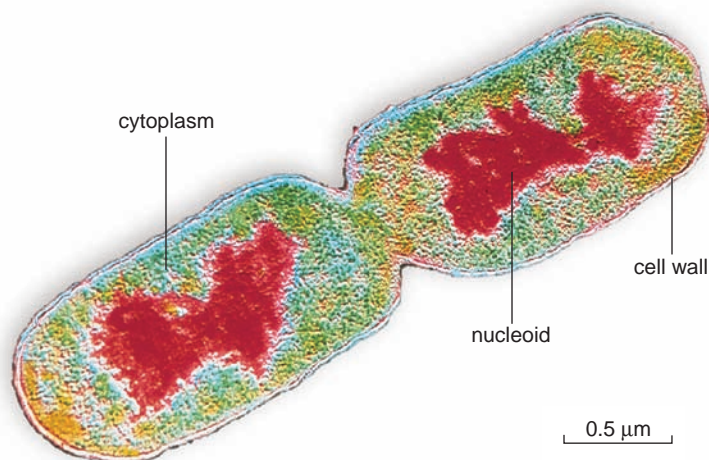


FIGURE 20.8 Binary fission.

When conditions are favorable for growth, prokaryotes divide to reproduce. This is a form of asexual reproduction because the daughter cells have exactly the same genetic material as the parent cell.

20.3 The Bacteria

Bacteria (domain Bacteria) are the more common type of prokaryote. The number of species of bacteria is amazing: To date, over 2,000 different bacteria have been named. They are found in practically every kind of environment on Earth.

Characteristics of Bacterial Cells

Most bacterial cells are protected by a cell wall that contains the unique molecule **peptidoglycan**. Peptidoglycan is a complex of polysaccharides linked by amino acids. Groups of bacteria are commonly differentiated from one another by using the Gram stain procedure, which was developed in the late 1880s by Hans Christian Gram, a Danish bacteriologist. Even today, the Gram stain is usually the first test used in the identification of unknown bacteria. Gram-positive bacteria retain a dye-iodine complex and appear purple under the light microscope, while Gram-negative bacteria do not retain the complex and appear pink. This difference is dependent on the construction of the cell wall—that is, the Gram-positive bacteria have a thick layer of peptidoglycan in their cell walls, whereas Gram-negative bacteria have only a thin layer. *Clostridium tetani*, which causes tetanus, is an example of a Gram-positive bacterium. *Vibrio cholerae*, which infects the small intestine and causes cholera, is an example of a Gram-negative bacterium.

Bacteria (and archaea) can also be described in terms of their three basic cell shapes (Fig. 20.9): spirilli (sing., spirillum), spiral-shaped or helical-shaped; bacilli (sing., bacillus), rod-shaped; and cocci (sing., coccus), round or spherical. These three basic shapes may be augmented by particular arrangements or shapes of cells. For example, rod-shaped prokaryotes may appear as very short rods (coccobacilli) or as very long filaments (fusiform). Cocci may form pairs (diplococci), chains (streptococci), or clusters (staphylococci).

Bacterial Metabolism

Bacteria are astoundingly diverse in terms of their metabolic lifestyles. With respect to basic nutrient requirements, bacteria are not much different from other organisms. One difference, however, concerns the need for oxygen. Some bacteria are **obligate anaerobes** and are unable to grow in the presence of free oxygen. A few serious illnesses—such as botulism, gas gangrene, and tetanus—are caused by anaerobic bacteria that infect oxygen-free environments in the human body, such as the intestine or deep puncture wounds. Other bacteria, called **facultative anaerobes**, are able to grow in either the presence or the absence of gaseous oxygen. Most bacteria, however, are aerobic and, like animals, require a constant supply of oxygen to carry out cellular respiration.

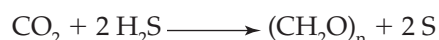
Autotrophic Bacteria

Bacteria called **photoautotrophs** [Gk. *photos*, light, *auto*, self, and *trophe*, food] are photosynthetic. They use solar energy to reduce carbon dioxide to organic compounds. There are two types of photoautotrophic bacteria: those that evolved first

and do not give off oxygen (O₂) and those that evolved later and do give off oxygen. Their characteristics are shown here:

Do Not Give Off O ₂	Do Give Off O ₂
Photosystem I only	Photosystems I and II
Unique type of chlorophyll called bacteriochlorophyll	Type of chlorophyll <i>a</i> found in plants

Green sulfur bacteria and some purple bacteria carry on the first type of photosynthesis. These bacteria usually live in anaerobic conditions, such as the muddy bottom of a marsh, and they cannot photosynthesize in the presence of oxygen. They do not give off oxygen because they do not use water as an electron donor; instead, they can, for example, use hydrogen sulfide (H₂S).



In contrast, the cyanobacteria (see Fig. 20.12) contain chlorophyll *a* and carry on photosynthesis in the second way, just as algae and plants do.



Bacteria called **chemoautotrophs** [Gk. *chemo*, pertaining to chemicals, *auto*, self, and *trophe*, food] carry out chemosynthesis. They oxidize inorganic compounds such as hydrogen gas, hydrogen sulfide, and ammonia to obtain the necessary energy to reduce CO₂ to an organic compound. The nitrifying bacteria oxidize ammonia (NH₃) to nitrites (NO₂⁻) and nitrites to nitrates (NO₃⁻). Their metabolic abilities keep nitrogen cycling through ecosystems. Other bacteria oxidize sulfur compounds. They live in environments such as deep-sea vents 2.5 km below sea level. The organic compounds produced by such bacteria and also archaea (discussed on page 369) support the growth of a community of organisms found at vents. This discovery lends support to the suggestion that the first cells originated at deep-sea vents.

Heterotrophic Bacteria

Bacteria called **chemoheterotrophs** [Gk. *chemo*, pertaining to chemicals, *hetero*, different, and *trophe*, food] take in organic nutrients. They are aerobic **saprotrophs** that decompose almost any large organic molecule to smaller ones that can be absorbed. There is probably no natural organic molecule that cannot be digested by at least one prokaryotic species. In ecosystems, saprotrophic bacteria are called decomposers. They play a critical role in recycling matter and making inorganic molecules available to photosynthesizers.

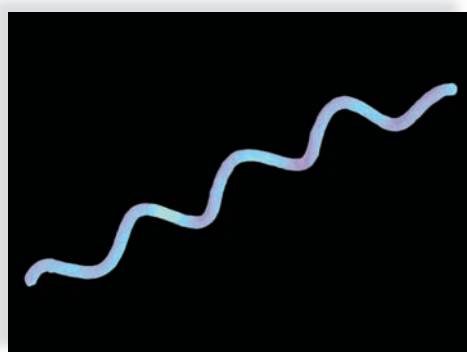
The metabolic capabilities of chemoheterotrophic bacteria have long been exploited by human beings. Bacteria are used commercially to produce chemicals, such as ethyl alcohol, acetic acid, butyl alcohol, and acetones. Bacterial action is also involved in the production of butter, cheese, sauerkraut, rubber, cotton, silk, coffee, and cocoa. Even antibiotics are produced by some bacteria.

Symbiotic Relationships

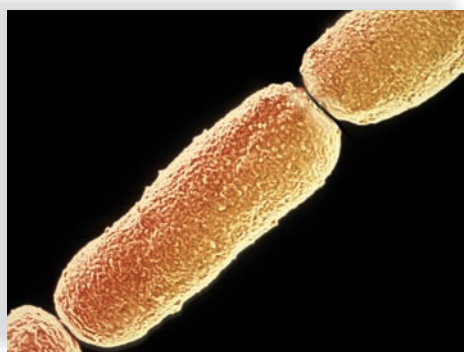
Bacteria (and archaea) form **symbiotic relationships** [Gk. *sym*, together, and *bios*, life] in which two different species live together in an intimate way. When the relationship is *mutualistic*, both species benefit. In *commensalistic* relationships, only one species benefits, and when it is *parasitic*, one species benefits but the other is harmed.

Commensalism often occurs when one population modifies the environment in such a way that a second population benefits. Obligate anaerobes can live in our intestines only because the bacterium *Escherichia coli* uses up the available oxygen. The parasitic bacteria cause disease, including human diseases.

Mutualistic bacteria live in human intestines, where they release vitamins K and B₁₂, which we can use to help produce blood components. In the stomachs of cows and goats, special mutualistic prokaryotes digest cellulose, enabling these animals to feed on grass. Mutualistic bacteria live in the root nodules of soybean, clover, and alfalfa plants where they reduce atmospheric



a. Spirillum: *Spirillum volutans* SEM 3,520×



b. Bacilli: *Bacillus anthracis* SEM 35,000×



c. Cocci: *Streptococcus thermophilus* SEM 6,250×

FIGURE 20.9 Diversity of bacteria.

a. Spirillum, a spiral-shaped bacterium. b. Bacilli, rod-shaped bacteria. c. Cocci, round bacteria.

a. © Dr. Richard Kessel & Dr. Gene Shih/Visuals Unlimited.

nitrogen (N_2) to ammonia, a process called nitrogen fixation (Fig. 20.10). Plants are unable to fix atmospheric nitrogen, and those without nodules take up nitrate and ammonia from the soil.

Parasitic bacteria cause diseases, and therefore are called **pathogens**. Some of the deadliest pathogens form **endospores** [Gk. *endon*, within, and *spora*, seed] when faced with unfavorable environmental conditions. A portion of the cytoplasm and a copy of the chromosome dehydrate and are then encased by a heavy, protective endospore coat (Fig. 20.11). In some bacteria, the rest of the cell deteriorates, and the endospore is released. Endospores survive in the harshest of environments—desert heat and dehydration, boiling temperatures, polar ice, and extreme ultraviolet radiation. They also survive for very long periods. When anthrax endospores 1,300 years old germinate, they can still cause a severe infection (usually seen in cattle and sheep). Humans also fear a deadly but uncommon type of food poisoning called botulism that is caused by the germination of endospores inside cans of food. To germinate, the endospore absorbs water and grows out of the endospore coat. In a few hours' time, it becomes a typical bacterial cell, capable of reproducing once again by binary fission. Endospore formation is not a means of reproduction, but it does allow survival and dispersal of bacteria to new places.

Many other bacteria cause diseases in humans: A few are listed in Table 20.2. In almost all cases, the growth of microbes themselves does not cause disease; the poisonous substances they release, called **toxins**, cause disease. When Gram-negative bacteria are killed by an antibiotic, the cell wall releases toxins called lipopolysaccharide fragments, and the result may be a high fever and a drop in blood pressure. Other bacteria secrete toxins when they are living. Some of these have a needle-shaped secretion apparatus they can use to inject toxins directly into host cells!

When someone steps on a rusty nail, bacteria can be injected deep into damaged tissue. The damaged area does

FIGURE 20.10 Nodules of a legume.

While some free-living bacteria carry on nitrogen fixation, those of the genus *Rhizobium* invade the roots of legumes, with the resultant formation of nodules. Here the bacteria convert atmospheric nitrogen to an organic nitrogen that the plant can use. These are nodules on the roots of a soybean plant, *Glycine*.

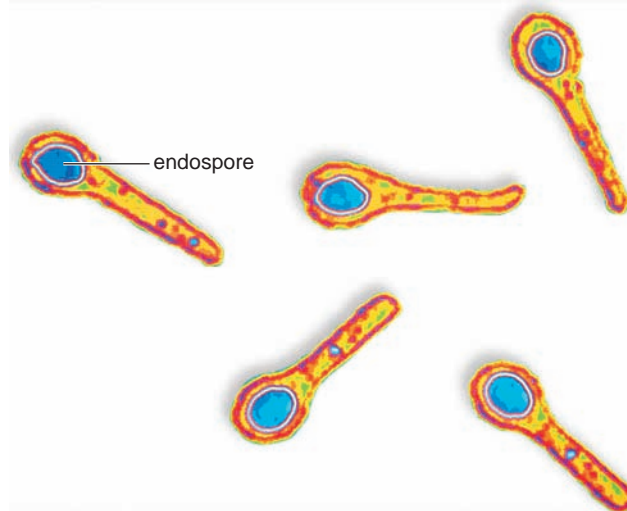
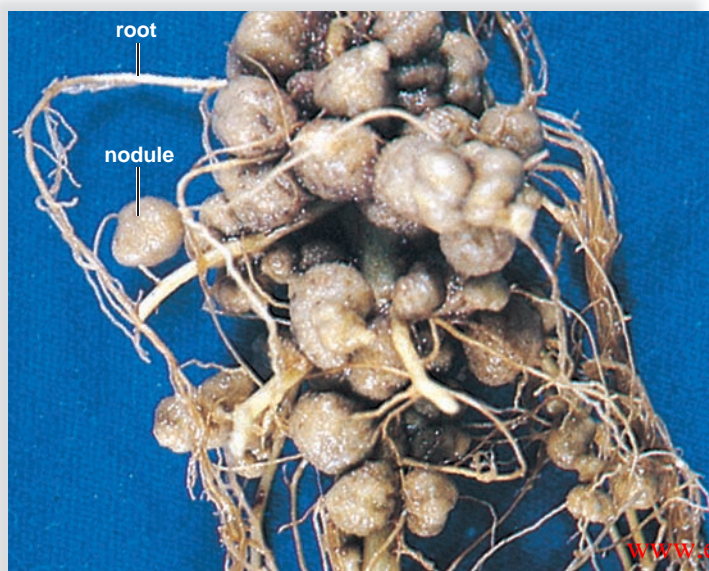


FIGURE 20.11 The endospore of *Clostridium tetani*.

C. tetani produces a terminal endospore that causes it to have a drumstick appearance. If endospores gain access to a wound, they germinate and release bacteria that produce a neurotoxin. The patient develops tetanus, a progressive rigidity that can result in death; immunization can prevent tetanus.

not have a good blood flow and can become anaerobic. The endospores of *Clostridium tetani* germinate and produce a toxin that causes tetanus. The bacteria never leave the site of the wound, but the tetanus toxin they produce does move throughout the body. This toxin prevents the relaxation of muscles. In time, the body contorts because all the muscles have contracted. Eventually, suffocation occurs.

Fimbriae allow a pathogen to bind to certain cells, and this determines which organs or cells of the body will be its host. Like many bacteria that cause dysentery (severe diarrhea), *Shigella dysenteriae* is able to stick to the intestinal wall. In addition, *S. dysenteriae* produces a toxin called Shiga toxin that increases the potential for fatality. Also, invasive mechanisms that give a pathogen the ability to move through tissues and into the bloodstream result in a more medically significant disease than if it were localized. Usually a person can recover from food poisoning caused by *Salmonella*. But some strains of *Salmonella* have virulence factors—including a needle-shaped

TABLE 20.2

Bacterial Diseases in Humans

Category	Disease
Sexually transmitted diseases	Syphilis, gonorrhea, chlamydia
Respiratory diseases	Strep throat, scarlet fever, tuberculosis, pneumonia, Legionnaires disease, whooping cough, inhalation anthrax
Skin diseases	Erysipelas, boils, carbuncles, impetigo, acne, infections of surgical or accidental wounds and burns, leprosy (Hansen disease)
Digestive tract diseases	Gastroenteritis, food poisoning, dysentery, cholera, peptic ulcers, dental caries
Nervous system diseases	Botulism, tetanus, leprosy, spinal meningitis
Systemic diseases	Plague, typhoid fever, diphtheria
Other diseases	Tularemia, Lyme disease

toxin secretion apparatus—that allow the bacteria to penetrate the lining of the colon and move beyond this organ. Typhoid fever, a life-threatening disease, can then result.

Antibiotics

Because bacteria are cells in their own right, a number of antibiotic compounds are active against bacteria and are widely prescribed. Most antibacterial compounds fall within two classes, those that inhibit protein biosynthesis and those that inhibit cell wall biosynthesis. Erythromycin and tetracyclines can inhibit bacterial protein synthesis because bacterial ribosomes function somewhat differently than eukaryotic ribosomes. Cell wall biosynthesis inhibitors generally block the formation of peptidoglycan, required to maintain bacterial integrity. Penicillin, ampicillin, and fluoroquinolone (like Cipro) inhibit bacterial cell wall biosynthesis without harming animal cells.

One problem with antibiotic therapy has been increasing bacterial resistance to antibiotics. Genes conferring resistance to antibiotics can be transferred between infectious bacteria by transformation, conjugation, or transduction. When penicillin was first introduced, less than 3% of *Staphylococcus aureus* strains were resistant to it. Now, due to selective advantage, 90% or more are resistant to penicillin and, increasingly, to methicillin, an antibiotic developed in 1957 (see page 283).

Cyanobacteria

Cyanobacteria [Gk. *kyanos*, blue, and *bacterion*, rod] are Gram-negative bacteria with a number of unusual traits. They photosynthesize in the same manner as plants and are believed to be responsible for first introducing oxygen into the primitive atmosphere. Formerly, the cyanobacteria were called blue-green algae and were classified with eukaryotic algae, but now they are classified as prokaryotes. Cyanobacteria can have other pigments that mask the color of chlorophyll so that they appear red, yellow, brown, or black, rather than only blue-green.

Cyanobacterial cells are rather large, ranging from 1 to 50 μm in width. They can be unicellular, colonial, or filamentous. Cyanobacteria lack any visible means of locomotion, although

some glide when in contact with a solid surface and others oscillate (sway back and forth). Some cyanobacteria have a special advantage because they possess heterocysts, which are thick-walled cells without nuclei, where nitrogen fixation occurs. The ability to photosynthesize and also to fix atmospheric nitrogen (N_2) means that their nutritional requirements are minimal. They can serve as food for heterotrophs in ecosystems.

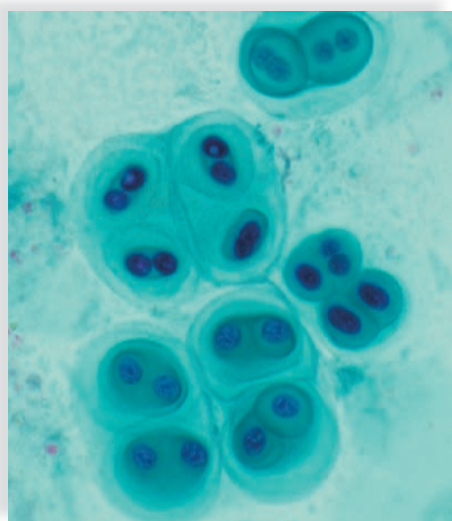
Cyanobacteria (Fig. 20.12) are common in fresh and marine waters, in soil, and on moist surfaces, but they are also found in harsh habitats, such as hot springs. They are symbiotic with a number of organisms, including liverworts, ferns, and even at times invertebrates such as corals. In association with fungi, they form **lichens** that can grow on rocks. In a lichen, cyanobacterium mutualistically provides organic nutrients to the fungus, while the fungus possibly protects and furnishes inorganic nutrients to the cyanobacterium. It is also possible that the fungus is parasitic on the cyanobacterium. Lichens help transform rocks into soil; other forms of life then may follow. It is hypothesized that cyanobacteria were the first colonizers of land during the course of evolution.

Cyanobacteria are ecologically important in still another way. If care is not taken in disposing of industrial, agricultural, and human wastes, phosphates drain into lakes and ponds, resulting in a “bloom” of these organisms. The surface of the water becomes turbid, and light cannot penetrate to lower levels. When a portion of the cyanobacteria die off, the decomposing prokaryotes use up the available oxygen, causing fish to die from lack of oxygen.

Check Your Progress

20.3

1. How is the peptidoglycan layer different in Gram-positive and Gram-negative cells?
2. What is the function of bacterial endospores?
3. Which bacteria produce much of the oxygen we breathe, and what metabolic process gives off this oxygen?



a. *Gloeocapsa*

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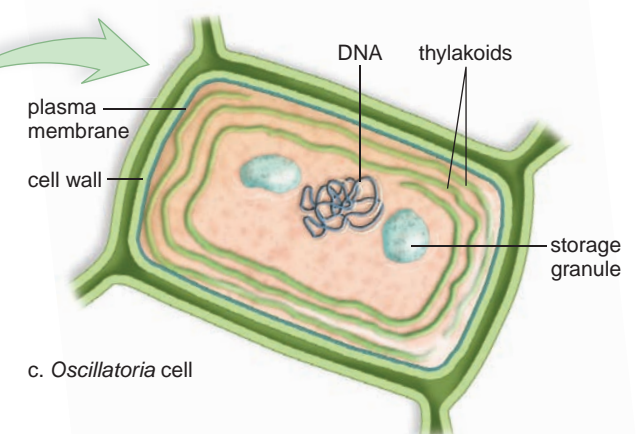


b. *Oscillatoria*

LM 100 \times

FIGURE 20.12 Diversity among the cyanobacteria.

a. In *Gloeocapsa*, single cells are grouped in a common gelatinous sheath. b. Filaments of cells occur in *Oscillatoria*. c. One cell of *Oscillatoria* as it appears through the electron microscope.



20.4 The Archaea

At one time, **archaea** (domain Archaea) were considered to be a unique group of bacteria. Archaea came to be viewed as a distinct domain of organisms in 1977, when Carl Woese and George Fox discovered that the rRNA of archaea has a different sequence of bases than the rRNA of bacteria. He chose rRNA because of its involvement in protein synthesis—any changes in rRNA sequence probably occur at a slow, steady pace as evolution occurs. As discussed in Chapter 19, it is proposed that the tree of life contains three domains: Archaea, Bacteria, and Eukarya. Because archaea and some bacteria are found in extreme environments (hot springs, thermal vents, salt basins), they may have diverged from a common ancestor relatively soon after life began. Then later, the eukarya diverged from the archaeal line of descent. In other words, the eukarya are more closely related to the archaea than to the bacteria. Archaea and eukarya share some of the same ribosomal proteins (not found in bacteria), initiate transcription in the same manner, and have similar types of tRNA.

Structure of Archaea

Archaea are prokaryotes with biochemical characteristics that distinguish them from both bacteria and eukaryotes. The plasma membranes of archaea contain unusual lipids that allow many of them to function at high temperatures. The lipids of archaea contain glycerol linked to branched-chain hydrocarbons in contrast to the lipids of bacteria, which contain glycerol linked to fatty acids. The archaea also evolved diverse cell wall types, which facilitate their survival under extreme conditions. The cell walls of archaea do not contain peptidoglycan as do the cell walls of bacteria. In some archaea, the cell wall is largely composed of polysaccharides, and in others, the wall is pure protein. A few have no cell wall.

Types of Archaea

Archaea were originally discovered living in extreme environmental conditions. Three main types of archaea are still distinguished based on their unique habitats: methanogens, halophiles, and thermoacidophiles (Fig. 20.13).

Methanogens

The **methanogens** (methane makers) are obligate anaerobes found in environments such as swamps, marshes, and the intestinal tracts of animals. Methanogenesis, the ability to form methane (CH_4), is a type of metabolism performed only by some archaea. Methanogens are chemoautotrophs, using hydrogen gas (H_2) to reduce carbon dioxide (CO_2) to methane and couple the energy released to ATP production.



Methane, also called biogas, is released into the atmosphere, where it contributes to the greenhouse effect and global warming. About 65% of the methane found in our atmosphere is produced by these methanogenic archaea.

Methanogenic archaea may help us anticipate what life may be like on other celestial bodies. Consider, for instance,



a.



b.



c.

FIGURE 20.13 Extreme habitats.

a. Halophilic archaea can live in salt lakes. **b.** Thermoacidophilic archaea can live in the hot springs of Yellowstone National Park. **c.** Methanogens live in swamps and in the guts of animals.

the unusual microbial community residing in the Lidy Hot Springs of eastern Idaho. The springs, which originate 200 m (660 feet) beneath the Earth's surface, are lacking in organic nutrients, but rich in H_2 . Scientists have found the springs to be inhabited by vast numbers of microorganisms; over 90%

are archaea, and the overwhelming majority are methanogens. The researchers who first investigated the Lidy Hot Springs microbes point out that similar methanogenic communities may someday be found beneath the surfaces of Mars and Europa (one of Jupiter's moons). Since hydrogen is the most abundant element in the universe, it would be readily available for use by methanogens everywhere.

Halophiles

The **halophiles** require high salt concentrations (usually 12–15%—the ocean is about 3.5% salt) for growth. They have been isolated from highly saline environments in which few organisms are able to survive, such as the Great Salt Lake in Utah, the Dead Sea, solar salt ponds, and hypersaline soils. These archaea have evolved a number of mechanisms to survive in environments that are high in salt. This survival ability benefits the halophiles, as they do not have to compete with as many microorganisms as they would encounter in a more moderate environment. The proteins of halophiles have unique chloride pumps that use halorhodopsin (related to the rhodopsin pigment found in our eyes) to pump chloride to the inside of the cell, and this prevents water loss. These organisms are aerobic chemoheterotrophs. However, some species can carry out a unique form of photosynthesis if their oxygen supply becomes scarce, as commonly occurs in highly saline conditions. Instead of chlorophyll, these halophiles use a purple pigment called bacteriorhodopsin to capture solar energy for use in ATP synthesis. Interestingly, most halophiles are so adapted to a high-saline environment that they perish if placed in a solution with a low salt concentration (such as pure water).

Thermoacidophiles

A third major type of archaea are the **thermoacidophiles**. These archaea are isolated from extremely hot, acidic environments such as hot springs, geysers, submarine thermal vents, and around volcanoes. They are chemoautotrophic anaerobes that use hydrogen (H_2) as the electron donor, and sulfur (S) or sulfur compounds as terminal electron acceptors, for their electron transport chains. Hydrogen sulfide

(H_2S) and protons (H^+) are common products.



Recall that the greater the concentration of protons, the lower (and more acidic) the pH. Thus, it is not surprising that thermoacidophiles grow best at extremely low pH levels, between pH 1 and 2. Due to the unusual lipid composition of their plasma membranes, thermoacidophiles survive best at temperatures above $80^\circ C$; some can even grow at $105^\circ C$ (remember that water boils at $100^\circ C$)!

Archaea in Moderate Habitats

Although archaea are capable of living in extremely stressful conditions, they are found in all moderate environments as well. For example, some archaea have been found living in symbiotic relationships with animals, including sponges and sea cucumbers. Such relationships are sometimes mutualistic or even commensalistic, but there are no parasitic archaea—that is, they are not known to cause infectious diseases.

The roles of archaea in activities such as nutrient cycling are still being explored. For example, a group of nitrifying marine archaea has recently been discovered. Some scientists think that these archaea may be major contributors to the supply of nitrite in the oceans. Nitrite can be converted by certain bacteria to nitrate, a form of nitrogen that can be used by plants and other producers to construct amino acids and nucleic acids. Archaea have also been found inhabiting lake sediments, rice paddies, and soil, where they are likely to be involved in nutrient cycling.

Check Your Progress

20.4

1. How are archaea different from bacteria?
2. List the three types of archaea distinguished by their unique habitats.
3. Archaea are thought to be closely related to eukaryotes. What evidence supports this possibility?
4. In a recent United Nations report, the practice of maintaining large herds of livestock was blamed for contributing to greenhouse gases. What is the basis for this claim?

Connecting the Concepts

Microbiology began when Leeuwenhoek first used his microscope to observe microorganisms. Significant advances occurred with the discovery that bacteria and viruses cause disease, and again when microbes were first used in genetic studies. Although there are significant structural differences between prokaryotes and eukaryotes, many biochemical similarities exist between the two. Thus, the details of protein synthesis, first worked out in bacteria, are applicable to all cells, including human cells. Today, transgenic bacteria routinely make products and otherwise serve the needs of human beings.

Many prokaryotes can live in environments that may represent the kinds of habitats available when the Earth first formed. We find prokaryotes in such hostile habitats as swamps, the Dead Sea, and hot sulfur springs. The fossil record suggests that the prokaryotes evolved before the eukaryotes. Not only do all living things trace their ancestry to the prokaryotes, but prokaryotes are believed to have contributed to the evolution of the eukaryotic cell. The mitochondria and chloroplasts of the eukaryotic cell are probably derived from bacteria that took up residence inside a nucleated cell.

Cyanobacteria are credited with introducing oxygen into the Earth's ancestral atmosphere, and they may have been the first colonizers of the terrestrial environment. Some bacteria are decomposers that recycle nutrients in both aquatic and terrestrial environments. Bacteria and archaea play significant roles in the carbon, nitrogen, and phosphorus cycles. Mutualistic bacteria also fix nitrogen in plant nodules, enabling herbivores to digest cellulose, and release certain vitamins in the human intestine. Clearly, humans are dependent on the past and present activities of prokaryotes.

summary

20.1 Viruses, Viroids, and Prions

Viruses are noncellular, while prokaryotes are fully functioning organisms. All viruses have at least two parts: an outer capsid composed of protein subunits and an inner core of nucleic acid, either DNA or RNA, but not both. Some also have an outer membranous envelope.

Viruses are obligate intracellular parasites that can be maintained only inside living cells, such as those of a chicken egg, or those propagated in cell (tissue) culture.

The lytic cycle of a bacteriophage consists of attachment, penetration, biosynthesis, maturation, and release. In the lysogenic cycle of a bacteriophage, viral DNA is integrated into bacterial DNA for an indefinite period of time, but it can undergo the lytic cycle when stimulated.

The reproductive cycle differs for animal viruses. Uncoating is needed to free the genome from the capsid, and either budding or lysis releases the viral particles from the cell. Retroviruses have an enzyme, reverse transcriptase, that carries out reverse transcription. This enzyme produces one strand of DNA (cDNA) using viral RNA as a template, and then another DNA strand that is complementary to the first one. The resulting double-strand DNA becomes integrated into host DNA. The AIDS virus is a retrovirus.

Viruses cause various diseases in plants and animals, including human beings. Viroids are naked strands of RNA (not covered by a capsid) that can cause disease in plants. Prions are protein molecules that have a misshapen tertiary structure. Prions cause diseases such as CJD in humans and mad cow disease in cattle when they cause other proteins of their own kind also to become misshapen.

20.2 The Prokaryotes

The bacteria (domain Bacteria) and archaea (domain Archaea) are prokaryotes. Prokaryotic cells lack a nucleus and most of the other cytoplasmic organelles found in eukaryotic cells. Prokaryotes reproduce asexually by binary fission. Their chief method for achieving genetic variation is mutation, but genetic recombination by means of conjugation, transformation, and transduction has been observed.

Prokaryotes differ in their need (and tolerance) for oxygen. There are obligate anaerobes, facultative anaerobes, and aerobic prokaryotes. Some prokaryotes are autotrophic, and some are heterotrophic.

20.3 The Bacteria

Bacteria (domain Bacteria) are the more prevalent type of prokaryote. The classification of bacteria is still being developed. Of primary importance at this time are the shape of the cell and the structure of the cell wall, which affects Gram staining. Bacteria occur in three basic shapes: spiral-shaped (spirillum), rod-shaped (bacillus), and round (coccus).

Some prokaryotes are autotrophic—either photoautotrophs (photosynthetic) or chemoautotrophs (chemosynthetic). Some photosynthetic bacteria (cyanobacteria) give off oxygen, and some (purple and green sulfur bacteria) do not. Chemoautotrophs oxidize inorganic compounds such as hydrogen gas, hydrogen sulfide, and ammonia to acquire energy to make their own food. Surprisingly, chemoautotrophs support communities at deep-sea vents.

Many bacteria are chemoheterotrophs (aerobic heterotrophs) and are saprotrophic decomposers that are absolutely essential to the cycling of nutrients in ecosystems. Their metabolic capabilities are so vast that they are used by humans both to dispose of and to

produce substances. Many heterotrophic bacteria are symbiotic. The mutualistic nitrogen-fixing bacteria live in nodules on the roots of legumes. Of special interest are the cyanobacteria, which were the first organisms to photosynthesize in the same manner as plants. When cyanobacteria are symbionts with fungi, they form lichens. Some bacterial symbionts, however, are parasitic and cause plant and animal, including human, diseases. Certain bacteria form endospores, which are extremely resistant to destruction. Their genetic material can thereby survive unfavorable conditions.

20.4 The Archaea

The archaea (domain Archaea) are a second type of prokaryote. On the basis of rRNA sequencing, it is thought that there are three evolutionary domains: Bacteria, Archaea, and Eukarya. In addition, the archaea appear to be more closely related to the eukarya than to the bacteria. Archaea do not have peptidoglycan in their cell walls, as do the bacteria, and they share more biochemical characteristics with the eukarya than do bacteria.

Three types of archaea live under harsh conditions, such as anaerobic marshes (methanogens), salty lakes (halophiles), and hot sulfur springs (thermoacidophiles). Archaea are also found in moderate environments.

understanding the terms

archaea 368	lytic cycle 358
bacteria 364	methanogen 368
bacteriophage 358	nucleoid 363
binary fission 364	obligate anaerobe 364
capsid 357	pathogen 366
chemoautotroph 365	peptidoglycan 364
chemoheterotroph 365	photoautotroph 364
commensalism 365	plasmid 363
conjugation 364	prion 362
conjugation pilus 364	prokaryote 362
cyanobacteria 367	retrovirus 361
emerging virus 361	reverse transcriptase 361
endospore 366	saprotroph 365
facultative anaerobe 364	symbiotic relationship 365
fimbriae 363	thermoacidophile 369
flagellum (pl., flagella) 363	toxin 366
halophile 369	transduction 364
host specific 358	transformation 364
lichen 367	viroid 361
lysogenic cell 359	virus 356
lysogenic cycle 358	

Match the terms to these definitions:

- _____ Bacteriophage life cycle in which the virus incorporates its DNA into that of the bacterium; only later does it begin a lytic cycle, which ends with the destruction of the bacterium.
- _____ Organism that contains chlorophyll and uses solar energy to produce its own organic nutrients.
- _____ Organism that secretes digestive enzymes and absorbs the resulting nutrients back across the plasma membrane.
- _____ Relationship that could be mutualistic, commensalistic, or parasitic.
- _____ Type of prokaryote that is most closely related to the Eukarya.

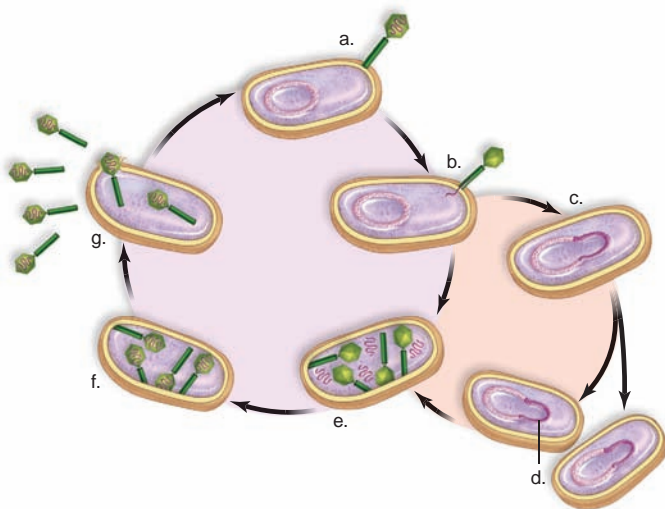
reviewing this chapter

- Describe the general structure of viruses, and describe both the lytic cycle and the lysogenic cycle of bacteriophages. 356–59
- Contrast viruses with cells in terms of the characteristics of life. 356–57
- How do animal viruses differ in structure and reproductive cycle? 359
- How do retroviruses differ from other animal viruses? Describe the reproductive cycle of retroviruses in detail. 361
- Explain Pasteur's experiment, which showed that bacteria do not arise spontaneously. 362
- Provide a diagram of prokaryotic cell structure and discuss. 362–64
- How do all prokaryotes introduce variations? How does genetic recombination occur in bacteria? 364
- How do all prokaryotes differ in their tolerance of and need for oxygen? 364–65
- Compare photosynthesis between the green sulfur bacteria and the cyanobacteria. 365, 367
- What are chemoautotrophic prokaryotes, and where have they been found to support whole communities? 365
- What role do endospores play in disease? 366
- Discuss the importance of cyanobacteria in ecosystems and in the history of the Earth. 367
- How do archaea differ from bacteria? 368–69
- What three different types of archaea may be distinguished based on their different habitats? 368–69

testing yourself

Choose the best answer for each question.

- Label this condensed version of bacteriophage reproductive cycles using these terms: penetration, maturation, release, prophage, attachment, biosynthesis, and integration.



- Viruses are considered nonliving because
 - they do not locomote.
 - they cannot reproduce independently.
 - their nucleic acid does not code for protein.
 - they are noncellular.
 - Both b and d are correct.

- Which of the following statements about viruses is incorrect?
 - The nucleic acid may be either DNA or RNA, but not both.
 - The capsid may be polyhedral or helical.
 - Viruses do not fit into the current system for naming organisms.
 - The nucleic acid may be either single stranded or double stranded.
 - Viruses are rarely, if ever, host specific.
- The envelope of an animal virus is derived from the _____ of its host cell.
 - cell wall
 - membrane
 - glycocalyx
 - receptors
- A prophage occurs during the reproduction cycle of
 - a lysogenic virus.
 - a poxvirus.
 - a lytic virus.
 - an enveloped virus.
- Which of these are found in all viruses?
 - envelope, nucleic acid, capsid
 - DNA, RNA, and proteins
 - proteins and a nucleic acid
 - proteins, nucleic acids, carbohydrates, and lipids
 - tail fibers, spikes, and rod shape
- Which would be the worst choice for cultivation of viruses?
 - tissue culture
 - bird embryos
 - live mammals
 - sterile broth
- A pathogen would most accurately be described as
 - a parasite.
 - a commensal.
 - a saprobe.
 - a symbiont.
- RNA retroviruses have a special enzyme that
 - disintegrates host DNA.
 - polymerizes host DNA.
 - transcribes viral RNA to cDNA.
 - translates host DNA.
 - produces capsid proteins.
- Which is not true of prokaryotes? They
 - are living cells.
 - lack a nucleus.
 - all are parasitic.
 - are both archaea and bacteria.
 - evolved early in the history of life.
- Facultative anaerobes
 - require a constant supply of oxygen.
 - are killed in an oxygenated environment.
 - do not always need oxygen.
 - are photosynthetic but do not give off oxygen.
 - All of these are correct.
- Which of these is most apt to be a prokaryotic cell wall function?
 - transport
 - motility
 - support
 - adhesion

13. Cyanobacteria, unlike other types of bacteria that photosynthesize, do
 - a. give off oxygen.
 - b. not have chlorophyll.
 - c. not have a cell wall.
 - d. need a fungal partner.
14. Chemoautotrophic prokaryotes
 - a. are chemosynthetic.
 - b. use the rays of the sun to acquire energy.
 - c. oxidize inorganic compounds to acquire energy.
 - d. are always bacteria, not archaea.
 - e. Both a and c are correct.
15. Archaea differ from bacteria in that
 - a. some can form methane.
 - b. they have different rRNA sequences.
 - c. they do not have peptidoglycan in their cell walls.
 - d. they rarely photosynthesize.
 - e. All of these are correct.
16. Which of these archaea would live at a deep-sea vent?
 - a. thermoacidophile
 - b. halophile
 - c. methanogen
 - d. parasitic forms
 - e. All of these are correct.
17. A prokaryote that can synthesize all its required organic components from CO_2 using energy from the sun is a
 - a. photoautotroph.
 - b. photoheterotroph.
 - c. chemoautotroph.
 - d. chemoheterotroph.
18. While testing some samples of marsh mud, you discover a new microbe that has never been described before. You examine it closely and find that, although it is cellular, there is no nucleus. Biochemical analysis reveals that the plasma membrane is made up of glycerol linked to branched-chain hydrocarbons, and the cell wall contains no peptidoglycan. This microbe is most likely a(n)
 - a. enveloped virus.
 - b. archaean.
 - c. prion.
 - d. bacterium.
 - e. bacteriophage.
19. The Nobel laureate Peter Medawar called a certain type of microbe “a piece of bad news wrapped up in protein.” Which of the following was he describing?
 - a. archaea
 - b. bacteria
 - c. prion
 - d. virus
 - e. viroid

thinking scientifically

1. While a few drugs are effective against some viruses, they often impair the function of body cells and thereby have a number of side effects. Most antibiotics (antibacterial drugs) do not cause side effects. Why would antiviral medications be more likely to produce side effects?
2. Model organisms are those widely used by researchers who wish to understand basic processes that are common to many species. Bacteria such as *Escherichia coli* are model organisms for modern geneticists. Compare the characteristics of bacteria to those of peas (see p. 287) and give three reasons why bacteria would be useful in genetic experiments.

bioethical issue

Identifying Carriers

Carriers of disease are persons who do not appear to be ill but can nonetheless pass on an infectious disease. The only way society can protect itself is to identify carriers and remove them from areas or activities where transmission of the pathogen is most likely. Sometimes it's difficult to identify all activities that might pass on a pathogen—for example, HIV. A few people believe that they have acquired HIV from their dentists, and while this is generally believed to be unlikely, medical personnel are still required to identify themselves when they are carriers of HIV.

Transmission of HIV is believed to be possible in certain sports. In a statistical study, the Centers for Disease Control and Prevention figured that the odds of acquiring HIV from another football player were 1 in 85 million. But the odds might be higher for boxing, a bloody sport. When two brothers, one of whom had AIDS, got into a vicious fight, the infected brother repeatedly bashed his head against his brother's. Both men bled profusely, and soon after, the previously uninfected brother tested positive for the virus. The possibility of transmission of HIV in the boxing ring has caused several states to require boxers to undergo routine HIV testing. If they are HIV positive, they can't fight.

Should all people who are HIV positive always be required to identify themselves, no matter what the activity? Why or why not? By what method would they identify themselves at school, at work, and in other places?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

<http://www.mhhe.com/maderbiology10>

21

Protist Evolution and Diversity

Protists are an astoundingly diverse collection of eukaryotic organisms that vary in form, lifestyle, nutrition, locomotion, and reproduction. The photosynthetic algae are ecological producers responsible for introducing copious amounts of oxygen into the atmosphere. Algae also have economic importance; for instance, the “nori” used to wrap sushi rolls is a red alga. Algin, another seaweed product, is a thickening ingredient in foods such as ice cream; it is also used in the production of pharmaceuticals, cosmetics, paper, and textiles—even the tungsten filaments of lightbulbs. Protozoans, which are heterotrophic and usually have a form of locomotion, serve as food for some animals but also cause diseases. Malaria is just one of several medically and economically important protozoan illnesses of humans.

The photo below shows a slime mold familiarly known as dog vomit, which creeps along the forest floor engulfing its food. In the nineteenth century, water molds caused a famine in Ireland by attacking potatoes and devastated the vineyards of France. In this chapter, we will see how diverse protists play essential roles in ecosystems, and how they directly affect our own species.

The so-called “dog vomit” slime mold (*Fuligo septica*) is a protist.

21.1 GENERAL BIOLOGY OF PROTISTS

- Protists are the first eukaryotic cells. They arose by a process of endosymbiosis. 374
- The protists are largely unicellular but are quite varied in structure, nutritional mode, and sexual life cycle. Some protists are photosynthetic, as are land plants; some are heterotrophic by ingestion, as are animals; and some are heterotrophic by absorption, as are fungi. 374–76

21.2 DIVERSITY OF PROTISTS

- The protists are placed in the following supergroups:

Archaeplastids include the land plants and the closest protistan relatives of land plants, the red algae and the green algae. 377–79

Chromalveolates, a mixed group, include the stramenopiles (with a hairy flagellum) and the alveolates (with alveoli beneath the plasma membrane). 381–85

Excavates include zooflagellates with atypical or absent mitochondria and distinctive flagella and/or a deep (excavated) oral groove. 386–87

Amoebozoans have pseudopods and no tests. 387–88

Rhizarians include the foramaniferans and radiolarians with pseudopods and tests. 388–89

Opisthokonts include fungi, animals, and the closest protistan relatives of animals, the choanoflagellates. 389



21.1 General Biology of Protists

Protists have eukaryotic cells characterized by membranous organelles. The endosymbiotic theory tells how an eukaryotic cell acquires mitochondria and chloroplasts. Mitochondria are derived from aerobic bacteria, and chloroplasts are derived from cyanobacteria that were engulfed on two separate occasions (Fig. 21.1a, b).

Protists vary in size from microscopic algae and protozoans to kelp that can exceed 200 m in length. Kelp, a brown alga, is multicellular; *Volvox*, a green alga, is colonial; while *Spirogyra*, also a green alga, is filamentous. Most protists are unicellular, but despite their small size they have attained a high level of complexity. The amoeboids and ciliates possess unique organelles—their contractile vacuole is an organelle that assists in water regulation.

Protists acquire nutrients in a number of different ways. We will see that the algae are photosynthetic and gather energy from sunlight. Many protozoans are heterotrophic, and some ingest food by endocytosis, thereby forming food vacuoles. A slime mold creeps along the forest floor ingesting decaying plant material in the same manner. Other protozoans are parasitic and absorb nutrient molecules meant for their host. Some protozoans, such as *Euglena*, are **mixotrophic**, meaning they are able to combine autotrophic and heterotrophic nutritional modes.

Asexual reproduction by mitosis is the norm in protists. Sexual reproduction involving meiosis and spore formation generally occurs only in a hostile environment. Spores are resistant to adverse conditions and can survive until favor-

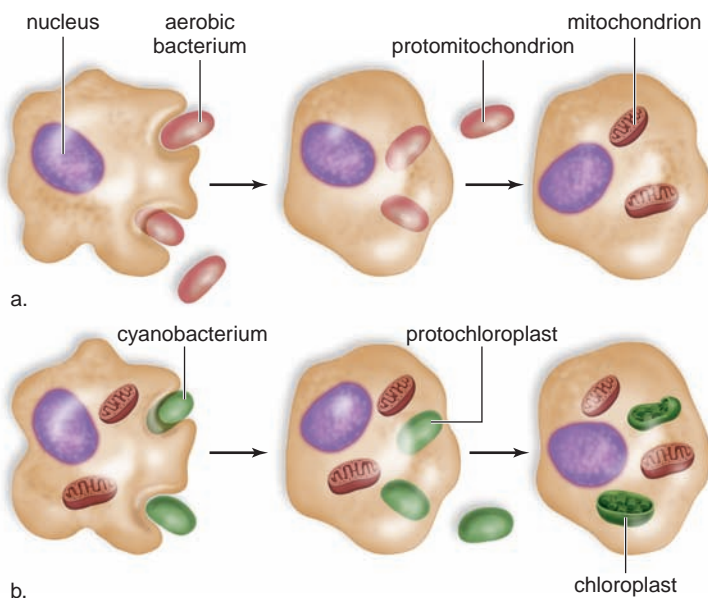


FIGURE 21.1 Origin of the eukaryotic cell.

The endosymbiotic theory tells us that mitochondria and chloroplasts were once free-living bacteria. **a.** A nucleated cell takes in aerobic bacteria, which become its mitochondria. **b.** A nucleated cell with mitochondria takes in photosynthetic bacteria (cyanobacteria), which become its chloroplasts.

able conditions return once more. Some protozoans form **cysts**, another type of resting stage. In parasites, a cyst often serves as a means of transfer to a new host.

While the protists have great medical importance because several cause diseases in humans, they also are of enormous ecological importance. Being aquatic, the photosynthesizers give off oxygen and function as producers in both freshwater and saltwater ecosystems. They are a part of **plankton** [Gk. *plankt*, wandering], organisms that are suspended in the water and serve as food for heterotrophic protists and animals.

Protists enter symbiotic relationships ranging from parasitism to mutualism. Coral reef formation is greatly aided by the presence of a symbiotic photosynthetic protist that lives in the tissues of coral animals, for example.

Evolution and Diversity of Protists

For convenience, the protists can be characterized according to modes of nutrition. The protists known as **algae** are autotrophic, as are land plants. Certain of the algae share a common ancestor with land plants, as is stressed in Chapter 23. The protozoans and slime molds tend to be heterotrophic by ingestion, as are animals. Certain of the protozoans are closely related to animals, as is discussed in Chapter 28. Water molds are heterotrophic by absorption, as are fungi, but they are probably not closely related to fungi.

The term **protozoan** can be somewhat ambiguous; some prefer to restrict the term to unicellular heterotrophic organisms that ingest their food. Or, the term can mean any unicellular (or colonial) eukaryote. In that case, protozoans include photosynthetic, heterotrophic, and mixotrophic organisms. Most protozoans have some form of locomotion, either by flagella, pseudopods, or cilia, and those that don't locomote tend to be parasitic. At one time, zoologists classified protozoans as animals.

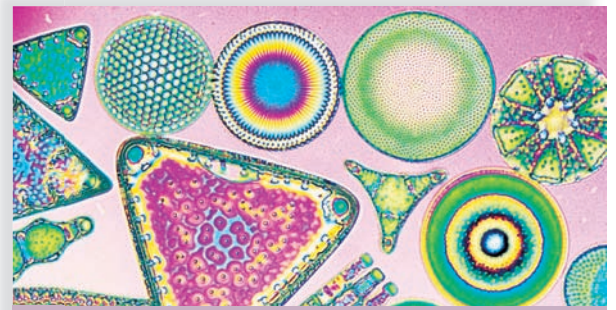
New research in the evolution of protists is overturning traditional taxonomical schemes. At this time, the most widely accepted formal approach for categorizing protists is to assign these diverse organisms to supergroups, as noted in the table in Figure 21.2. A **supergroup** is a major eukaryotic group, and the table designates six supergroups that encompass all members of the domain Eukarya, including the protists, plants, fungi, and animals. The relationship of the supergroups based on molecular studies is shown in Figure 21.3.

Check Your Progress

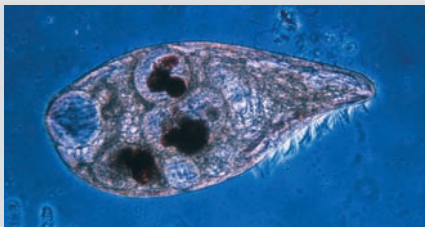
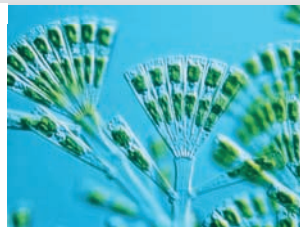
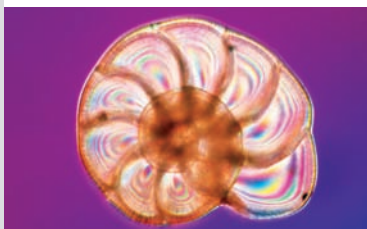
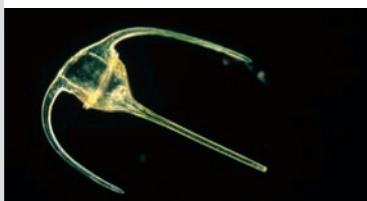
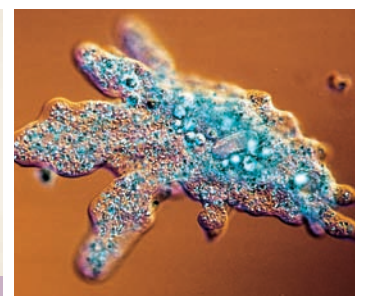
21.1

1. Which major group of organisms was the first to have eukaryotic cells?
2. How are algae and protozoans nutritionally different from one another?
3. **a.** Which supergroup includes both plants and protists?
b. Which includes fungi and animals, as well as protists?

DOMAIN: Eukarya Protists		
CHARACTERISTICS Usually a complex single cell; photosynthesize, ingest, or absorb food; haploid life cycle		
Supergroup	Members	Distinguishing Features
Archaeplastids	Green algae, red algae, land plants, charophytes	Plastids; unicellular, colonial, and multicellular
Chromalveolates	Stramenopiles: brown algae, diatoms, golden brown algae, water molds Alveolates: ciliates, apicomplexans, dinoflagellates	Most with plastids; unicellular and multicellular Alveoli support plasma membrane; unicellular
Excavates	Euglenids, kinetoplastids, parabasalids, diplomonads	Feeding groove; unique flagella; unicellular
Amoebozoans	Amoeboids, plasmodial and cellular slime molds	Pseudopods; unicellular
Rhizarians	Foraminiferans, radiolarians	Thin pseudopods; some with tests; unicellular
Opisthokonts	Choanoflagellates, animals, nucleariids, fungi	Some with flagella; unicellular and colonial



Assorted fossilized diatoms

*Onychodromus*, a giant ciliate ingesting one of its own kind*Plasmodium*, a slime mold*Blepharisma*, a ciliate with visible vacuoles*Licmorpha*, a stalked diatom*Nonionina*, a foraminiferan*Acetabularia*, a single-celled green alga (chlorophyte)*Ceratium*, an armored dinoflagellate*Bossiella*, a coralline red alga*Synura*, a colony-forming golden brown alga*Amoeba proteus*, a protozoan**FIGURE 21.2** Protist diversity.

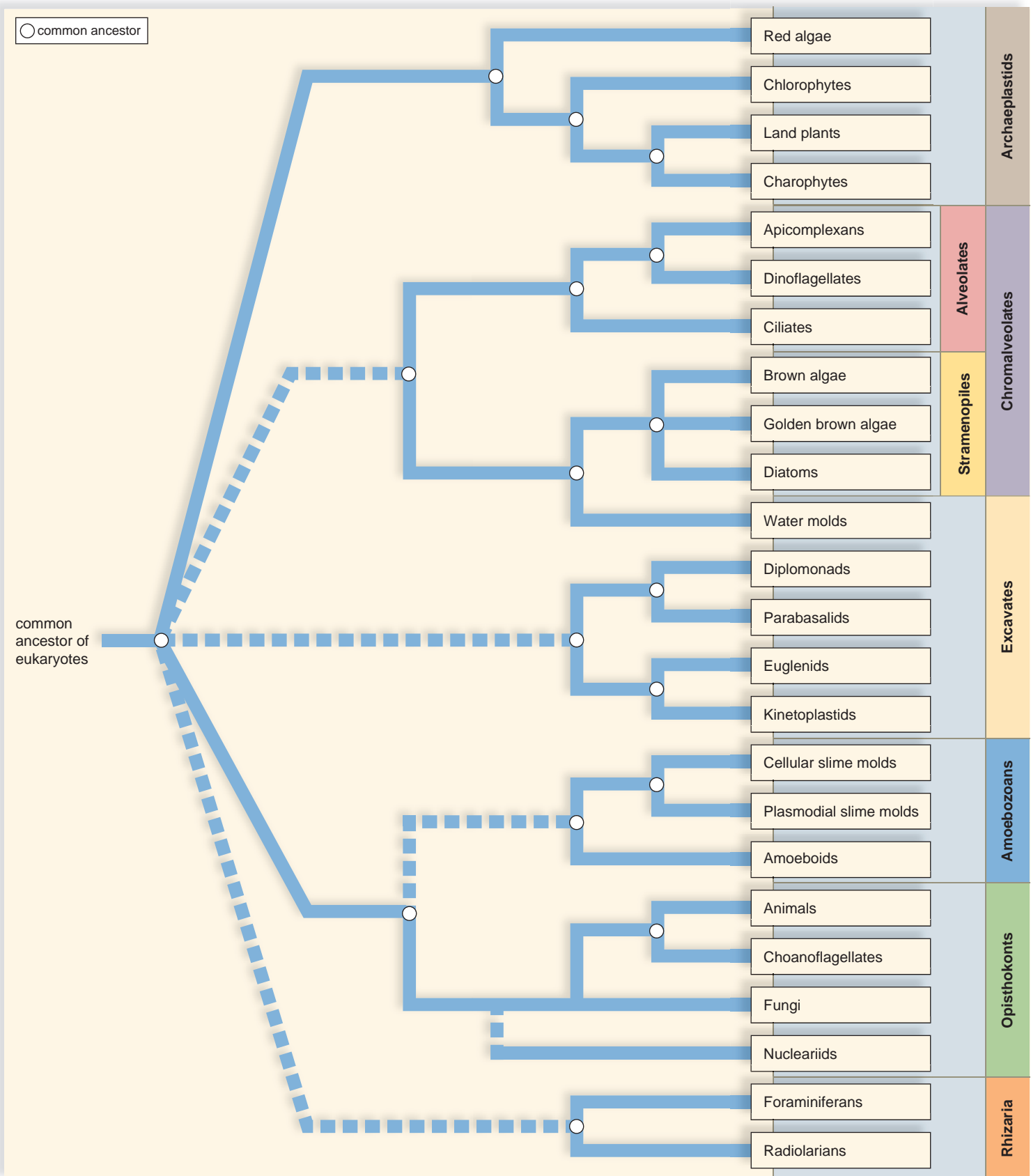


FIGURE 21.3 Evolutionary relationships between the eukaryotic supergroups.

Molecular data are used to determine the relatedness of the supergroups and their constituents. The dashed lines indicate relationships that are not certain at this time. This is a simplified tree that does not include all members of each supergroup.

21.2 Diversity of Protists

Supergroup Archaeplastids

The **archaeplastids** (ARE key PLAS tids) [Gk. *archeos*, ancient, *plastikos*, moldable] include land plants and other photosynthetic organisms, such as green and red algae that have plastids derived from endosymbiotic cyanobacteria (see Fig. 21.1b).

Green Algae

The **green algae** are protists that contain both chlorophylls *a* and *b*. They inhabit a variety of environments, including oceans, freshwater environments, snowbanks, the bark of trees, and the backs of turtles. The green algae, which number 17,000 species, also form symbiotic relationships with fungi, plants, and animals. As discussed in Chapter 22, they associate with fungi in lichens. Green algae occur in an abundant variety of forms. The majority of green algae are unicellular; however, filamentous and colonial forms exist. Some multicellular green algae are seaweeds that resemble lettuce leaves. Despite the name, green algae are not always green; some possess additional pigments that give them an orange, red, or rust color.

Biologists have long suggested that land plants are closely related to the green algae because, in addition to chlorophylls *a* and *b*, both land plants and green algae have a cell wall that contains cellulose and store reserve food as starch. Based on molecular data, the green algae may be subdivided into the **chlorophytes** and the **charophytes**. As discussed in Chapter 23, the latter is thought to be the green algae group most closely related to land plants.

Chlorophytes. *Chlamydomonas* is a minute, actively moving chlorophyte that inhabits still, freshwater pools. Its fossil ancestors date back over a billion years. Because the alga

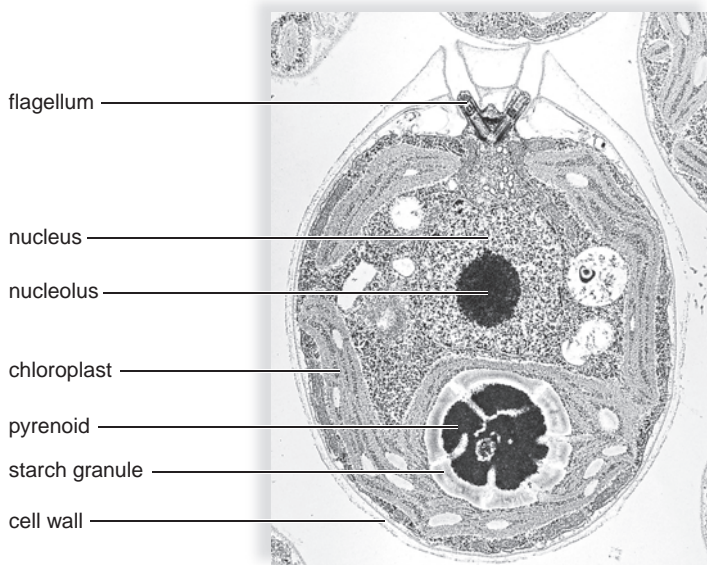


FIGURE 21.4 Electron micrograph of *Chlamydomonas*.

Chlamydomonas is a microscopic unicellular chlorophyte.

Chlamydomonas is less than 25 μm long, its anatomy is best seen in an electron micrograph (Fig. 21.4). It has a definite cell wall and a single, large, cup-shaped chloroplast that contains a *pyrenoid*, a dense body where starch is synthesized. In many species, a bright red eyespot is sensitive to light and helps bring the organism to locations favorable to photosynthesis. Two long, whiplike flagella projecting from the anterior end operate with a breaststroke motion.

Chlamydomonas most often reproduces asexually; mitosis produces as many as 16 daughter cells still within the parent cell wall (Fig. 21.5). Each daughter cell then secretes a cell wall and acquires flagella. The daughter cells escape by secreting an enzyme that digests the parent cell wall.

Chlamydomonas occasionally reproduces sexually when growth conditions are unfavorable. Gametes of two different mating types come into contact and join to form a zygote. A heavy wall forms around the zygote, and it becomes a resistant zygospore that undergoes a period of dormancy. When a zygospore germinates, it produces four zoospores by meiosis. **Zoospores**, which are flagellated spores typical of aquatic species, grow to become the adult.

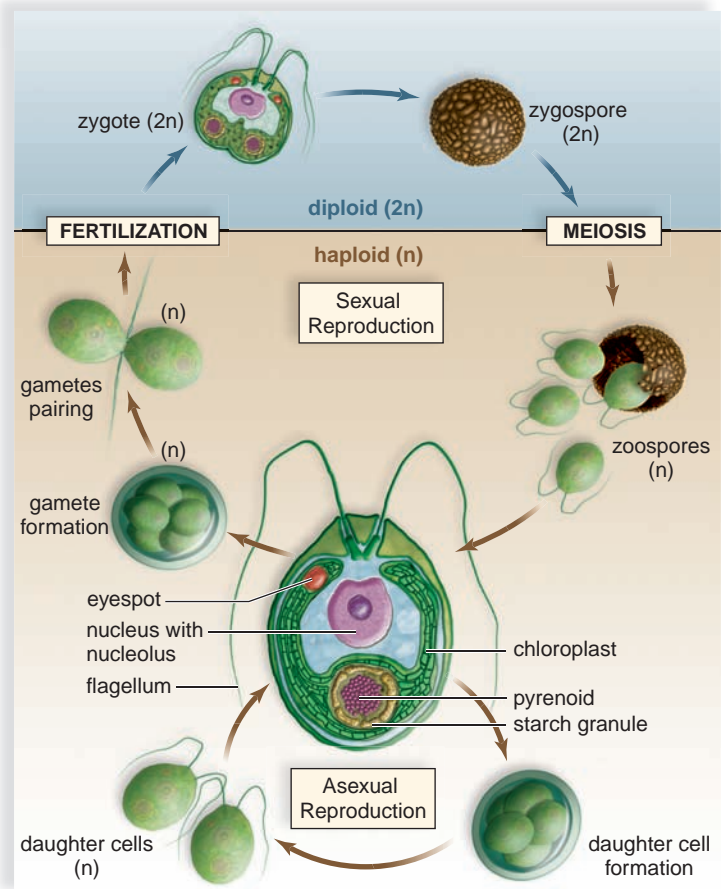


FIGURE 21.5 Reproduction in *Chlamydomonas*.

Chlamydomonas is motile because it has flagella. During asexual reproduction, all structures are haploid; during sexual reproduction, meiosis follows the zygospore stage, which is the only diploid part of the cycle.

A number of colonial forms occur among the flagellated chlorophytes. *Volvox* is a well-known colonial green alga. A **colony** is a loose association of independent cells. A *Volvox* colony is a hollow sphere with thousands of cells arranged in a single layer surrounding a watery interior. Each cell of a *Volvox* colony resembles a *Chlamydomonas* cell—perhaps it is derived from daughter cells that fail to separate following zoospore formation. In *Volvox*, the cells cooperate in that the flagella beat in a coordinated fashion. Some cells are specialized for reproduction, and each of these can divide asexually to form a new daughter colony (Fig. 21.6). This daughter colony resides for a time within the parent colony, but then it leaves by releasing an enzyme that dissolves away a portion of the parent colony, allowing it to escape.

Ulva is a multicellular chlorophyte, commonly called sea lettuce because it lives in the sea and has a leafy appearance

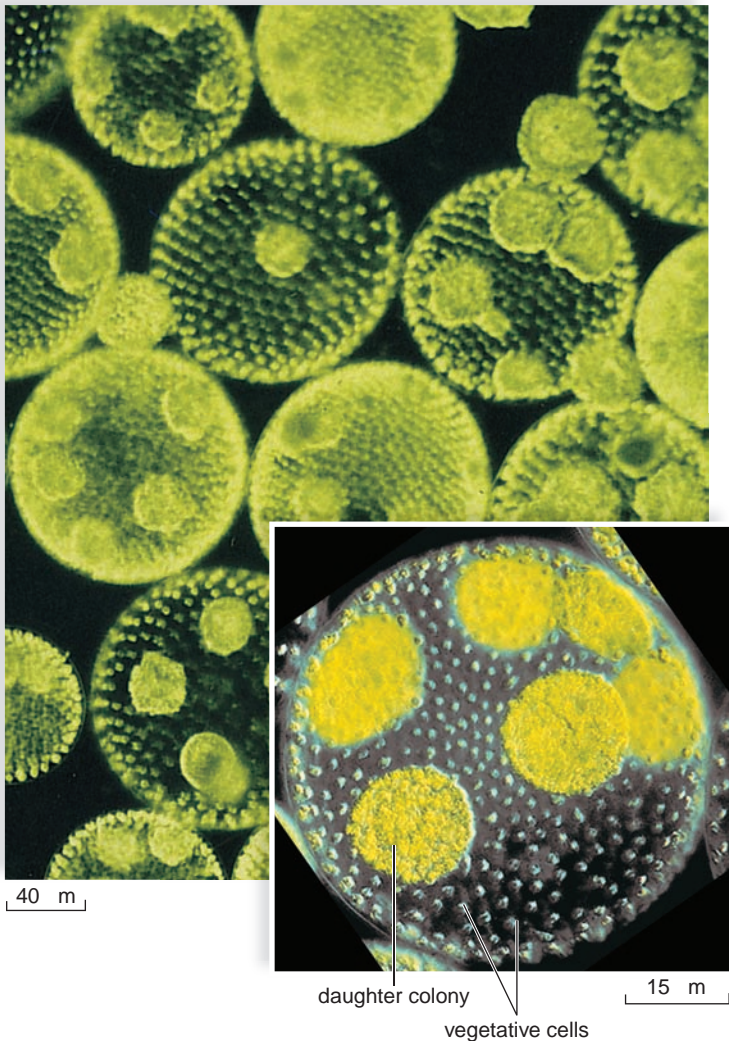


FIGURE 21.6 *Volvox*.

Volvox is a colonial chlorophyte. The adult *Volvox* colony often contains daughter colonies, which are asexually produced by special cells.



a. *Ulva*, several individuals



b. One individual

FIGURE 21.7 *Ulva*.

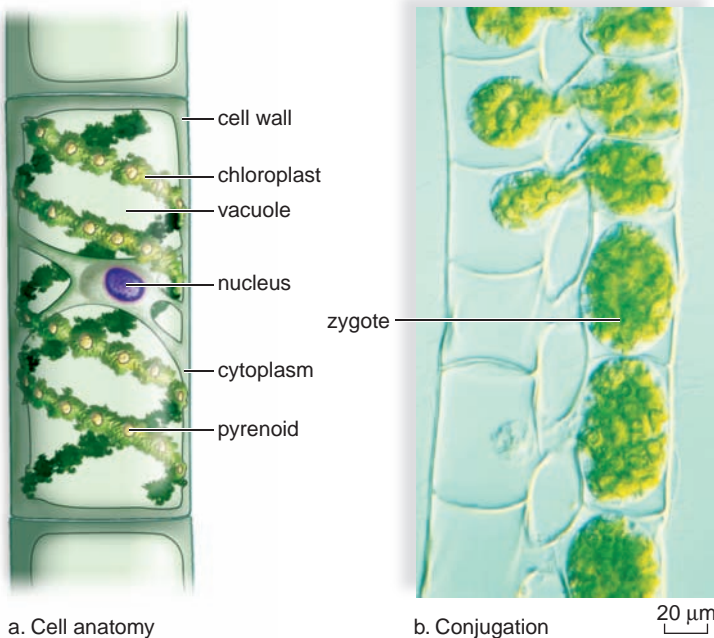
Ulva is a multicellular chlorophyte known as sea lettuce.

ance (Fig. 21.7). The thallus (body) is two cells thick and can be as much as a meter long. *Ulva* has an alternation of generations life cycle (see Fig. 21Ab, p. 380) like that of land plants, except that both generations look exactly alike, and the gametes all look the same.

Charophytes. **Filaments** [*L. filum*, thread] are end-to-end chains of cells that form after cell division occurs in only one plane. The charophytes are filamentous. In some, the filaments are branched, and in others the filaments are unbranched. *Spirogyra* is an unbranched charophyte. Charophytes often grow epiphytically on (but not taking nutrients from) aquatic flowering plants; they also attach to rocks or other objects underwater. Some are suspended in the water.

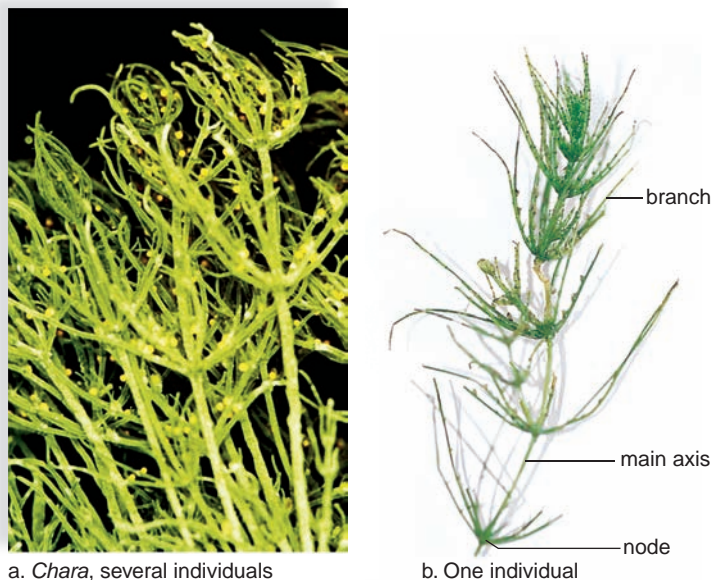
Spirogyra is found in green masses on the surfaces of ponds and streams. It has ribbonlike, spiralled chloroplasts (Fig. 21.8). During sexual reproduction, *Spirogyra* undergoes **conjugation** [*L. conjugal*, pertaining to marriage], a temporary union during which the cells exchange genetic material. The two filaments line up parallel to each other, and the cell contents of one filament move into the cells of the other filament, forming diploid zygotes. Resistant zygospores survive the winter, and in the spring they undergo meiosis to produce new haploid filaments.

Chara (Fig. 21.9) is a charophyte that lives in freshwater lakes and ponds. It is commonly called a stonewort because it is encrusted with calcium carbonate deposits. The main axis of the alga, which can be over a meter long, is a single file of very long cells anchored by rhizoids, which are colorless, hairlike filaments. Only the cell at the upper end of the main axis produces new cells. Whorls of branches occur at multicellular nodes, regions between the giant cells of the main axis. Each of the branches is also a single file of cells (Fig. 21.9b).

**FIGURE 21.8** *Spirogyra*.

a. *Spirogyra* is an unbranched charophyte in which each cell has a ribbonlike chloroplast. **b.** During conjugation, the cell contents of one filament enter the cells of another filament. Zygote formation follows.

Male and female multicellular reproductive structures grow at the nodes, and in some species they occur on separate individuals. The male structure produces flagellated sperm, and the female structure produces a single egg. The zygote is retained until it is enclosed by tough walls. DNA sequencing data suggest that among green algae, the stoneworts are most closely related to land plants, as is thoroughly discussed on pages 414–15.

**FIGURE 21.9** *Chara*.

Chara is an example of a stonewort, a charophyte that shares a common ancestor with land plants.

**FIGURE 21.10** Red alga.

Red algae are multicellular seaweeds, represented by *Rhodoglossum affine*.

Red Algae

The **red algae** are multicellular seaweeds that possess a red pigment (phycoerythrin) and a blue pigment (phycocyanin) in addition to chlorophyll (Fig. 21.10). These algae live primarily in warm seawater, growing in both shallow and deep waters. Some grow at depths exceeding 70 m, where their unique pigments allow them to absorb the few light rays that penetrate so deep.

The more than 5,000 species are quite variable; most are usually much smaller and more delicate than brown algae, but some species can exceed a meter in length. Red algae can be filamentous but more often they are complexly branched, with the branches having a feathery, flat, or expanded, ribbonlike appearance. Coralline algae are red algae that have cell walls impregnated with calcium carbonate. In some instances, coralline algae contribute as much to the growth of coral reefs as do coral animals.

Red algae are economically important. Agar is a gelatin-like product made primarily from the algae *Gelidium* and *Gracilaria*. Agar is used commercially to make capsules for vitamins and drugs, as a material for making dental impressions, and as a base for cosmetics. In the laboratory, agar is a solidifying agent for a bacterial culture medium. When purified, it becomes the gel for electrophoresis, a procedure that separates proteins or nucleotides. Agar is also used in food preparation—as an antidrying agent for baked goods and to make jellies and desserts set rapidly. Carrageenin, extracted from various red algae, is an emulsifying agent for the production of chocolate and cosmetics. *Porphyra*, a red alga, is the basis of a billion-dollar aquaculture industry in Japan. The reddish-black wrappings around sushi rolls consist of processed *Porphyra* blades.

Check Your Progress

21.2A

1. What feature of the haploid life cycle causes the adult *Chlamydomonas* to be haploid?
2. Of the archaeplastids studied, which are multicellular?

science focus

Life Cycles Among the Algae

Both asexual and sexual reproduction occur in algae, depending on species and environmental conditions. The types of life cycles seen in algae occur in other protists, and also in plants or animals.

Asexual reproduction is a frequent mode of reproduction among protists when the environment is favorable to growth. Asexual reproduction requires only one parent. The offspring are identical to this parent because the offspring receive a copy of only this parent's genes. The new individuals are likely to survive and flourish if the environment is steady. Various modes of asexual reproduction occur, but growth alone produces a new individual.

Sexual reproduction, with its genetic recombination due in part to fertilization and independent assortment of chromosomes, is more likely to occur among protists when the environment is changing and is unfavorable to growth. Recombination of genes might produce individuals that are more likely to survive

extremes in the environment—such as high or low temperatures, acidic or basic pH, or the lack of a particular nutrient.

Sexual reproduction requires two parents, each of which contributes chromosomes (genes) to the offspring by way of gametes. The gametes fuse to produce a diploid zygote. A reproductive cycle is isogamous when the gametes look alike—called isogametes—and a cycle is oogamous when the gametes are dissimilar—called heterogametes. Usually a small flagellated sperm fertilizes a large egg with plentiful cytoplasm.

Meiosis occurs during sexual reproduction—just when it occurs makes the sexual life cycles diagrammed in Figure 21A differ from one another. In these diagrams, the diploid phase is shown in blue, and the haploid phase is shown in tan. The haploid life cycle (Fig. 21Aa) most likely evolved first. In the haploid cycle, the zygote divides by meiosis to form haploid spores that develop into haploid individuals. In algae, the spores are typi-

cally zoospores. The zygote is only the diploid stage in this life cycle, and the haploid individual gives rise to gametes. This life cycle is seen in *Chlamydomonas* and a number of other algae.

In alternation of generations, the sporophyte ($2n$) produces haploid spores by meiosis (Fig. 21Ab). A spore develops into a haploid gametophyte that produces gametes. The gametes fuse to form a diploid zygote, and the zygote develops into the sporophyte. This life cycle is characteristic of some algae (e.g., *Ulva* and *Laminaria*) and all plants. In *Ulva*, the haploid and diploid generations have the same appearance. In plants, they are noticeably different from each other.

In the diploid life cycle, typical of animals, a diploid individual produces gametes by meiosis (Fig. 21Ac). Gametes are the only haploid stage in this cycle. They fuse to form a zygote that develops into the diploid individual. This life cycle is rare in algae but does occur in a few species of the brown alga *Fucus*.

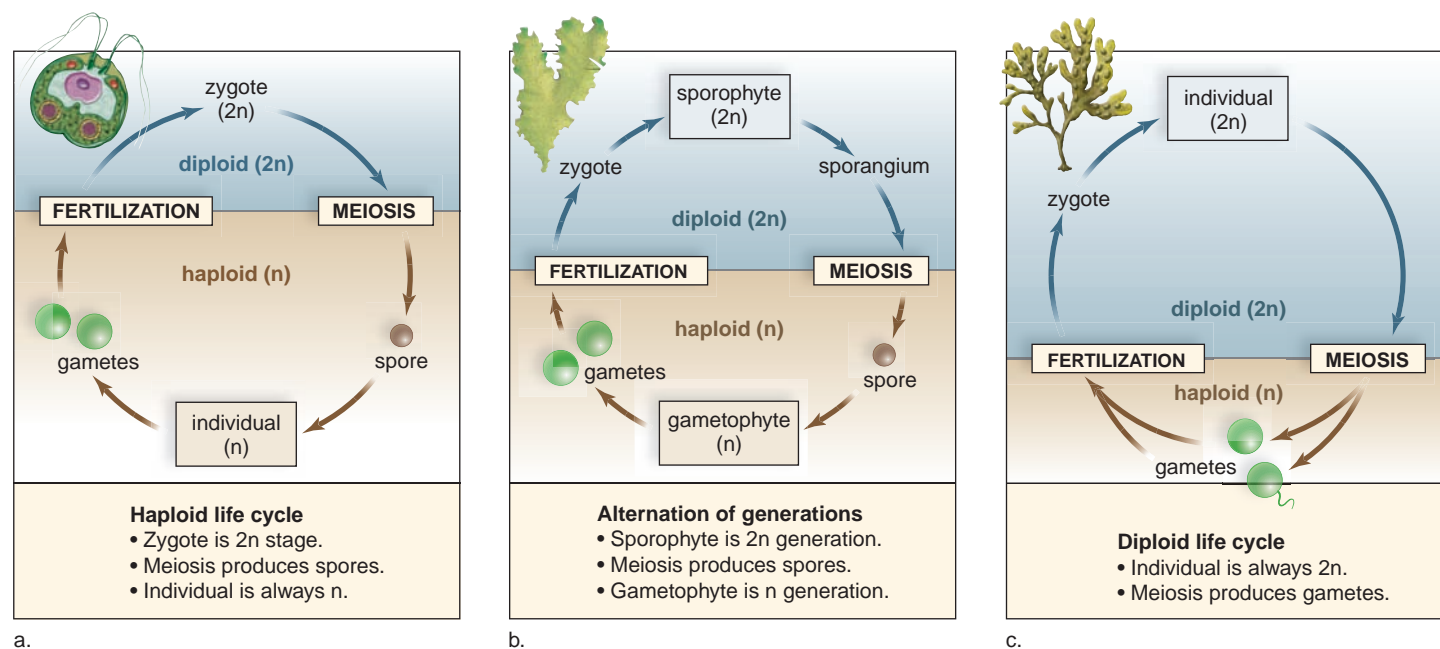


FIGURE 21A Common life cycles in sexual reproduction.

Supergroup Chromalveolates

The **chromalveolates** [Gk. *chroma*, color, L. *alveolus*, hollow] include two large subgroups: the stramenopiles and the alveolates.

Stramenopiles

The **stramenopiles** either have flagella or are descended from an ancestor that had flagella, one of which is longer than the other and covered with hairlike projections.

Brown Algae. The **brown algae** are stramenopiles that have chlorophylls *a* and *c* in their chloroplasts and a type of carotenoid pigment (fucoxanthin) that gives them their characteristic color. The reserve food is stored as a carbohydrate called *laminarin*. The brown algae range from small forms with simple filaments to large multicellular forms that may reach 100 m in length (Fig. 21.11). The vast majority of the 1,500 species live in cold ocean waters.

The multicellular brown algae are seaweeds often observed along the rocky coasts in the north temperate zone. They are pounded by waves as the tide comes in and are exposed to dry air as the tide goes out. They dry out slowly, however, because their cell walls contain a mucilaginous, water-retaining material.

Both *Laminaria*, commonly called *kelp*, and *Fucus*, known as *rockweed*, are examples of brown algae that grow along the shoreline. In deeper waters, the giant kelps (*Macrocystis* and *Nereocystis*) often

grow extensively in vast beds. Individuals of the genus *Sargassum* sometimes break off from their holdfasts and form floating masses. Brown algae not only provide food and habitat for marine organisms, they are harvested for human food and for fertilizer in several parts of the world. *Macrocystis* is the source of algin, a pectinlike material that is added to ice cream, sherbet, cream cheese, and other products to give them a stable, smooth consistency.

Laminaria is unique among the protists because members of this genus show tissue differentiation—that is, they transport organic nutrients by way of a tissue that resembles phloem in land plants. Most brown algae have the alternation of generations life cycle, but some species of *Fucus* are unique in that meiosis produces gametes, and the adult is always diploid, as in animals.

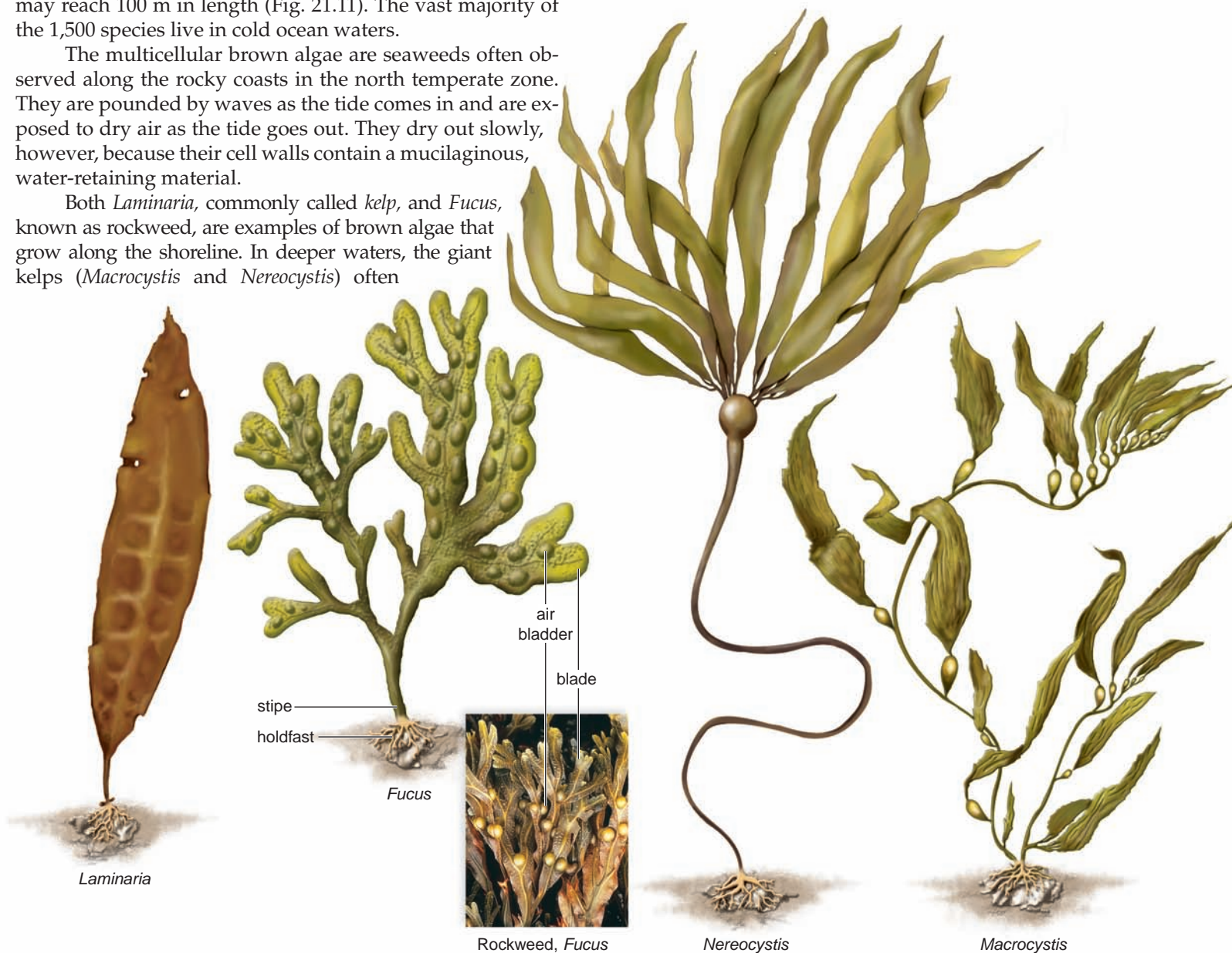


FIGURE 21.11 Brown algae.

Laminaria and *Fucus* are seaweeds known as kelps. They live along rocky coasts of the north temperate zone. The other brown algae featured, *Nereocystis* and *Macrocystis*, form spectacular underwater “forests” at sea.

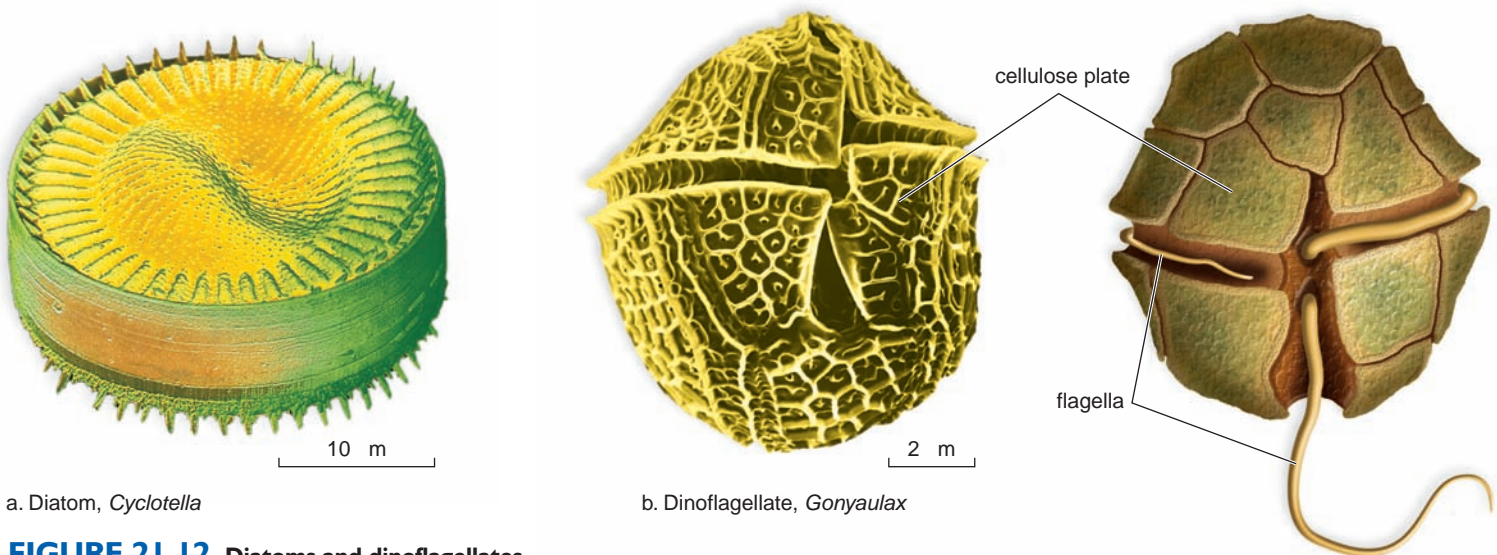


FIGURE 21.12 Diatoms and dinoflagellates.

a. Diatoms are stramenopiles of various colors, but even so their chloroplasts contain a unique golden brown pigment (*fucoxanthin*), in addition to chlorophylls *a* and *c*. The beautiful pattern results from markings on the silica-embedded wall. **b.** Dinoflagellates are alveolates, such as *Gonyaulax*, with cellulose plates.

Diatoms. A **diatom** [Gk. *dia*, through, and *temno*, cut] is a stramenopile that has an ornate silica shell resembling a petri dish—a top shell half, called a valve, fits over a lower valve (Fig. 21.12a). Diatoms have an orange-yellow color because they contain a carotenoid pigment in addition to chlorophyll. The approximately 100,000 species are a significant part of plankton serving as a source of oxygen and food for heterotrophs in both freshwater and marine ecosystems.

When diatoms reproduce asexually, each receives one old valve. The new valve fits inside the old one; therefore, new diatoms are smaller than the original ones. This continues until diatoms are about 30% of the original size. Then they reproduce sexually. The zygote becomes a structure that grows and then divides mitotically to produce diatoms of normal size.

The valves are covered with a great variety of striations and markings that form beautiful patterns when observed under the microscope. These are actually depressions or pores through which the organism makes contact with the outside environment. The remains of diatoms, called diatomaceous earth, accumulate on the ocean floor and are mined for use as filtering agents, soundproofing materials, and gentle polishing abrasives, such as those found in silver polish and toothpaste.

Golden Brown Algae. The **golden brown algae** derive their distinctive color from yellow-brown carotenoid pigments. The cells of these unicellular or colonial protists typically have two flagella that bear tubular hairs, which is characteristic of stramenopiles. Among the 1,000 species, the cells may be naked, covered with organic or silica scales, or enclosed in a secreted cage-like structure called a lorica. Many golden brown algae, such as *Ochromonas* (Fig. 21.13), are mixotrophs, a term that means they are both autotrophic and heterotrophic. *Ochromonas* is capable of photosynthesis

as well as phagocytosis. Like diatoms, the golden brown algae contribute to freshwater and marine phytoplankton.

Water Molds. The **water molds** usually live in the water, where they form furry growths when they parasitize fishes or insects and decompose remains. In spite of their common name, some water molds live on land and parasitize insects and plants. Nearly 700 species of water molds have been described. A water mold, *Phytophthora infestans*, was responsible for the 1840s potato famine in Ireland, and another, *Plasmopara viticola*, for the downy mildew of grapes that ravaged the vineyards of France in the 1870s. However, most

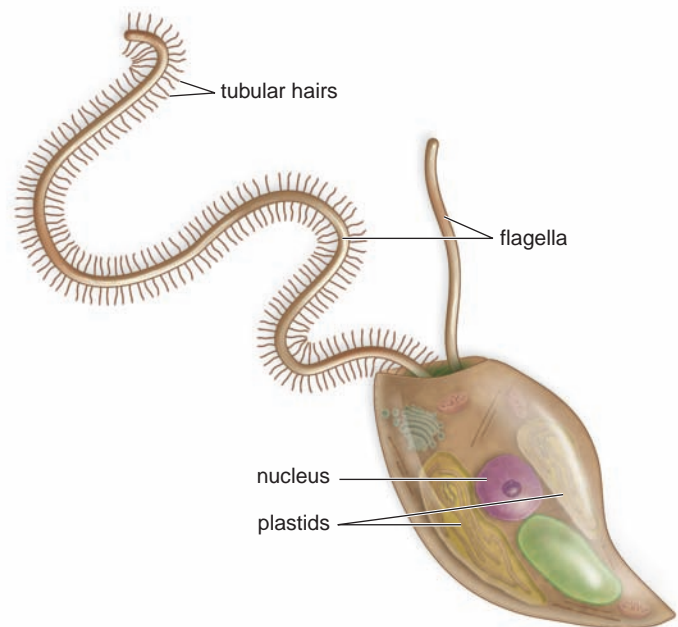


FIGURE 21.13 *Ochromonas*, a golden brown alga.

Golden brown algae have a type of flagella that characterizes the stramenopiles. The longer of the two flagella has rows of tubular hairs.

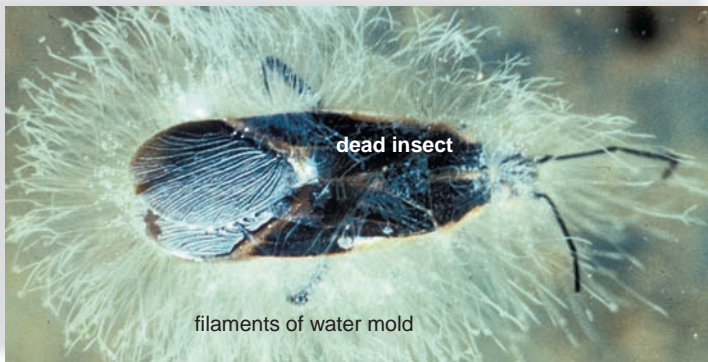


FIGURE 21.14 Water mold.

Saprolegnia, a water mold, feeding on a dead insect, is not a fungus.

water molds are saprotrophic and live off dead organic matter. Another well-known water mold is *Saprolegnia*, which is often seen as a cottonlike white mass on dead organisms (Fig. 21.14).

Water molds have a filamentous body as do fungi, but their cell walls are largely composed of cellulose, whereas fungi have cell walls of chitin. The life cycle of water molds differs from that of fungi. During asexual reproduction, water molds produce motile spores ($2n$ zoospores), which are flagellated. The organism is diploid (not haploid as in the fungi), and meiosis produces gametes. Their alternate name “oomycetes” refers to enlarged tips (called oogonia) where eggs are produced.

Check Your Progress

21.2B

1. Brown algae, diatoms, and water molds are dissimilar in appearance and way of life. Why are they all stramenopiles?
2. Which of the stramenopiles are you apt to find living on land?

Alveolates

The **alveolates** have alveoli (small sacs) lying just beneath their plasma membranes; the alveoli are thought to lend support to the cell surface. The alveolates are unicellular.

Dinoflagellates. The single cell of a **dinoflagellate** is usually bounded by protective cellulose plates impregnated with silicates (see Fig. 21.12b). Typically, they have two flagella; one lies in a longitudinal groove with its distal end free, and the other lies in a transverse groove that encircles the organism. The longitudinal flagellum acts as a rudder, and the beating of the transverse flagellum causes the cell to spin as it moves forward. The chloroplasts of a dinoflagellate vary in color from yellow-green to brown because, in addition to chlorophylls *a* and *c*, they contain carotenoids.

The approximately 4,000 species are diverse. Some species, such as *Noctiluca*, are capable of bioluminescence (producing light). Being a part of the plankton, the dinoflagellates are an important source of food for small animals in the ocean. They also live within the bodies of some invertebrates as symbionts. Symbiotic dinoflagellates lack cellulose plates and flagella and are called zooxanthellae. Corals (see Chapter 28), members of the animal kingdom, usually contain large numbers of zooxanthellae. They provide their hosts with organic nutrients, and the corals provide wastes that fertilize the algae. Photosynthetic dinoflagellates are often mixotrophs that can take in available food particles by phagocytosis.

Like the diatoms, dinoflagellates are one of the most important groups of producers in marine environments. Occasionally, however, they undergo a population explosion and become more numerous than usual. At these times, their density can equal 30,000 in a single milliliter. When dinoflagellates such as *Gymnodinium brevis* increase in number, they may cause a phenomenon called **red tide**. Massive fish kills can occur as the result of a powerful neurotoxin produced by these dinoflagellates (Fig. 21.15a). Humans who consume shellfish that have fed during a *Gymnodinium* outbreak may suffer from paralytic shellfish poisoning, in which the respiratory organs are paralyzed.

FIGURE 21.15 Fish kill and dinoflagellate bloom.

a. Fish kills, such as this one in University Lake in Baton Rouge, Louisiana, can be the result of a dinoflagellate bloom. **b.** This bloom, often called a red tide after the color of the water, appeared near California’s central coast.



a.



b.

Dinoflagellates usually reproduce asexually using mitosis and longitudinal division of the cell. A daughter cell gets half the cellulose plates unless they were shed before reproduction began. During sexual reproduction the daughter cells act as gametes. The zygote enters a resting stage broken when meiosis produces only one haploid cell because the others disintegrate.

Ciliates. The **ciliates** are unicellular protists that move by means of cilia. They are the most structurally complex and specialized of all protozoa. Members of the genus *Paramecium* are classic examples of ciliates (Fig. 21.16a). Hundreds of cilia, which beat in a coordinated rhythmic manner, project through tiny holes in a semirigid outer covering, or pellicle. Numerous oval capsules lying in the cytoplasm just beneath the pellicle contain **trichocysts**. Upon mechanical or chemical stimulation, trichocysts discharge long, barbed threads that are useful for defense and for capturing prey. Some trichocysts release poisons.

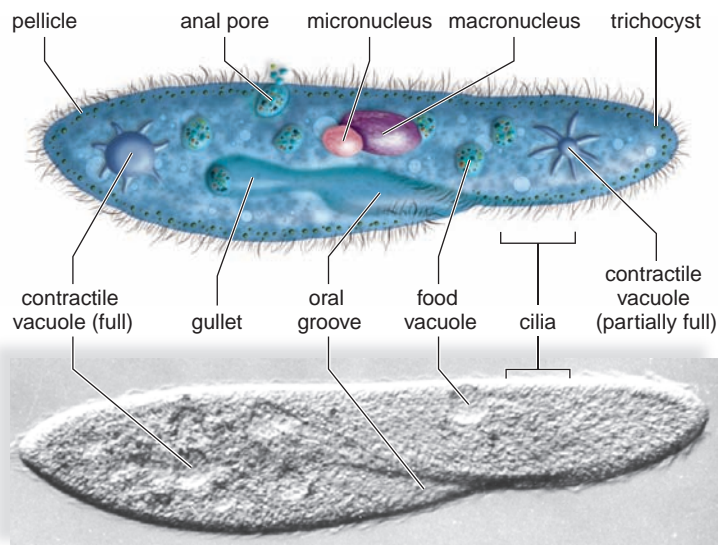
Most ciliates ingest their food. For example, when a paramecium feeds, food particles are swept down a gullet, below which food vacuoles form. Following digestion, the

soluble nutrients are absorbed by the cytoplasm, and the nondigestible residue is eliminated at the anal pore.

During asexual reproduction, ciliates divide by transverse binary fission. Ciliates have two types of nuclei: a large macronucleus and one or more small micronuclei. The macronucleus controls the normal metabolism of the cell, while the micronuclei are concerned with reproduction. Sexual reproduction involves conjugation (Fig. 21.16b). The macronucleus disintegrates and the micronuclei undergo meiosis. Two ciliates exchange haploid micronuclei. Then the micronuclei give rise to a new macronucleus, which contains copies of only certain housekeeping genes.

The ciliates are a diverse group of protozoans which range in size from 10 to 3,000 μm and number approximately 8,000 species. The majority of ciliates are free-living; however, several parasitic, sessile, and colonial forms exist. The barrel-shaped didiniums expand to consume paramecia much larger than themselves. *Suctorians* have an even more dramatic way of getting food. They rest quietly on a stalk until a hapless victim comes along. Then they promptly paralyze it and use their tentacles like straws to suck it dry. *Stentor* may be the most elaborate ciliate, resembling a giant blue vase decorated with stripes (Fig. 21.16c). *Ichthyophthirius* is responsible for a common disease in fishes called “ick.” If left untreated, it can be fatal.

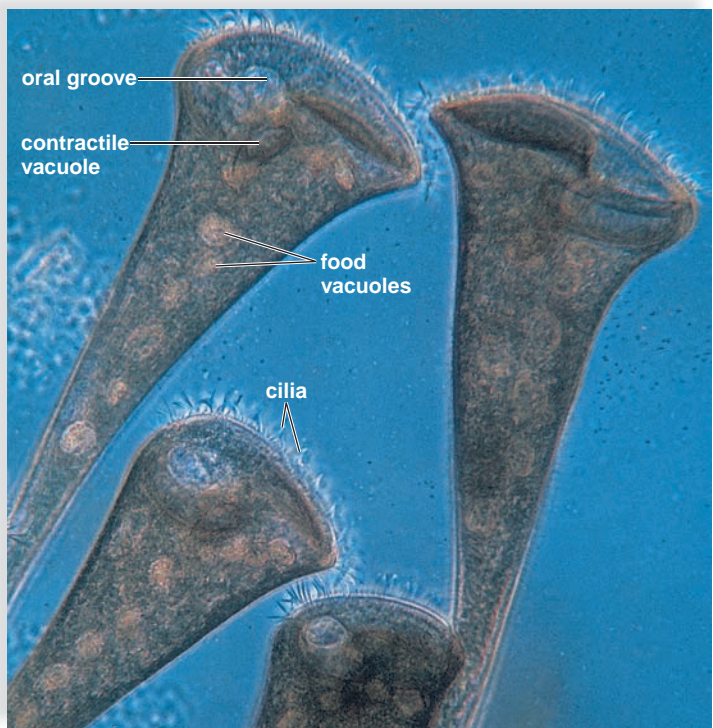
Apicomplexans. The **apicomplexans**, also known as *sporozoans*, are nearly 3,900 species of nonmotile, parasitic, spore-forming protozoans. All apicomplexans are parasites; the “apical complex” for which they are named is a unique collection of



a. *Paramecium*



b. During conjugation two paramecia first unite at oral areas



c. *Stentor*

FIGURE 21.16 Ciliates.

Ciliates are the most complex of the protists. **a.** Structure of *Paramecium*, adjacent to an electron micrograph. Note the oral groove, the gullet, and anal pore. **b.** A form of sexual reproduction called conjugation occurs periodically. **c.** *Stentor*, a large, vase-shaped, freshwater ciliate.

organelles at one end of the infective stage. Many apicomplexans have multiple hosts.

According to the CDC (Centers for Disease Control and Prevention), there are approximately 350–500 million cases of malaria worldwide; every year, more than a million people die of the infection. In humans, malaria is caused by four distinct members of the genus *Plasmodium*. *Plasmodium vivax*, the cause of one type of malaria, is the most common human parasite. The life cycle alternates between a sexual and an asexual phase in different hosts. Female *Anopheles* mosquitoes acquire protein for production of eggs by biting humans and other animals. When a human is bitten, the parasite eventually invades the red blood cells. The chills and fever of malaria appear when the infected cells burst and release toxic substances into the blood (Fig. 21.17). Despite

efforts to control the malaria parasite, as well as the mosquito vector, malaria is making a resurgence. International travel coupled with new resistant forms of both the parasite and the *Anopheles* mosquito is presenting health professionals with formidable problems.

Although the malarial parasite *Plasmodium* is the best known of the sporozoans, the apicomplexans include many examples of human parasites. *Pneumocystis carinii* causes the type of pneumonia seen primarily in AIDS patients. During sexual reproduction, thick-walled cysts form in the lining of pulmonary air sacs. The cysts contain spores that successively divide until the cyst bursts and the spores are released. Each spore becomes a new mature organism that can reproduce asexually but may also enter the sexual stage and form cysts. *Toxoplasma gondii*, another apicomplexan, causes toxoplasmosis, particularly in cats but also in people. In pregnant women, the parasite can infect the fetus and cause birth defects and mental retardation; in AIDS patients, it can infect the brain and cause neurological symptoms.

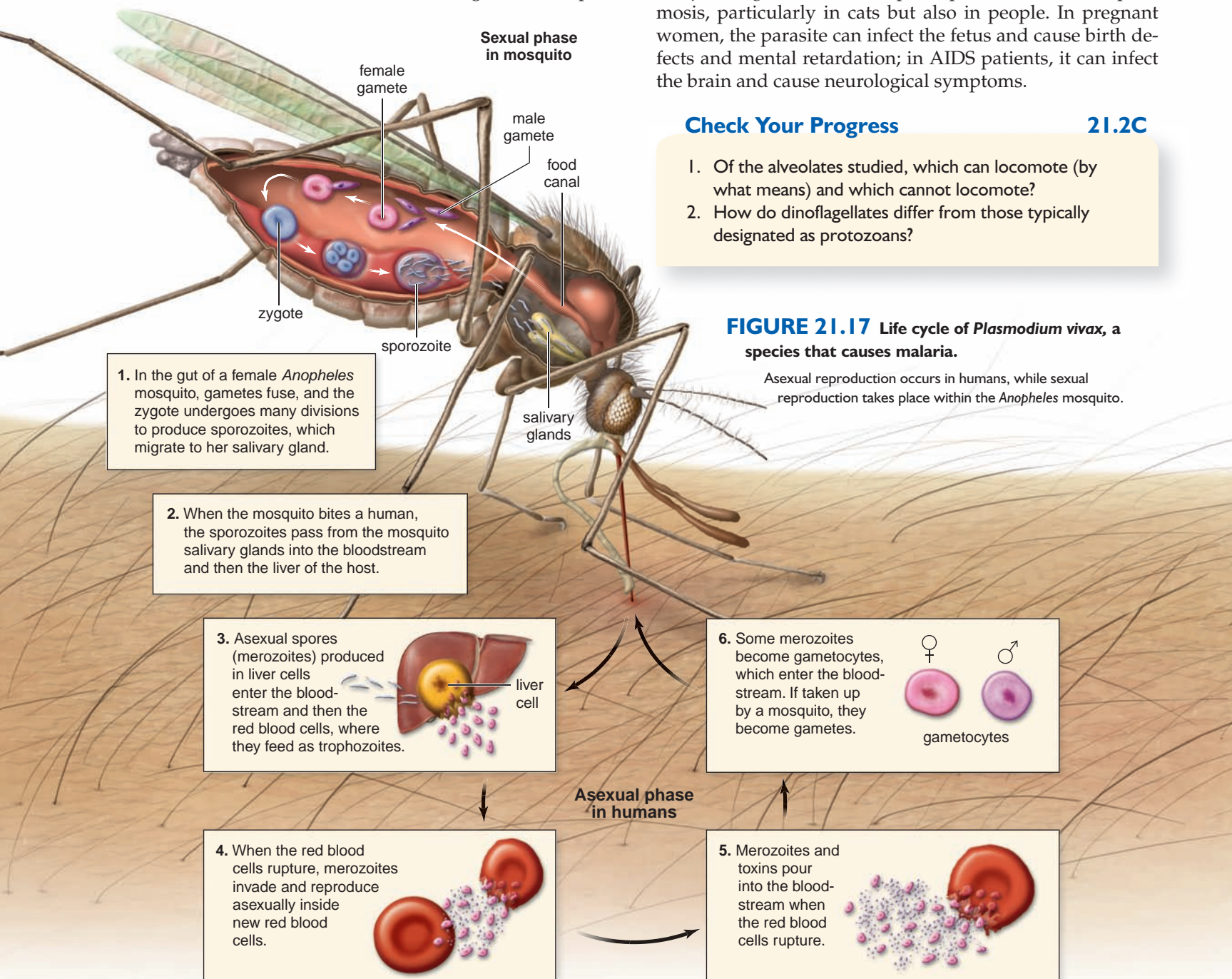
Check Your Progress

21.2C

1. Of the alveolates studied, which can locomote (by what means) and which cannot locomote?
2. How do dinoflagellates differ from those typically designated as protozoans?

FIGURE 21.17 Life cycle of *Plasmodium vivax*, a species that causes malaria.

Asexual reproduction occurs in humans, while sexual reproduction takes place within the *Anopheles* mosquito.



Supergroup Excavates

The **excavates** [L. *cavus*, hollow] include **zooflagellate** with atypical or absent mitochondria and distinctive flagella and/or deep (excavated) oral grooves.

Euglenids

The **euglenids** are small (10–500 μm), freshwater unicellular organisms. Attempts at classifying the approximately 1,000 species of euglenids typify the problem of classifying excavates, and indeed protists in general. One-third of all genera have chloroplasts; the rest do not. Those that lack chloroplasts ingest or absorb their food. This may not be surprising when one knows that their chloroplasts are like those of green algae and are probably derived from them through endosymbiosis. The chloroplasts are surrounded by three rather than two membranes. A pyrenoid is a special region of the chloroplast where carbohydrate formation occurs. Euglenids produce an unusual type of carbohydrate called paramylon.

A common euglenid is *Euglena decens*, an inhabitant of freshwater ditches and ponds. Because of the mixotrophic *Euglena*'s ability to undergo photosynthesis, as well as ingest food, this organism has been treated as a plantlike organism in botany texts and an animal-like organism in zoology texts. Euglenids have two flagella, one of which typically is much longer than the other and projects out of an anterior, vase-shaped invagination (Fig. 21.18). It is called a tinsel flagellum because it has hairs on it. Near the base of this flagellum is an eyespot, which shades a photoreceptor for detecting light. Because euglenids are bounded by a flexible *pellicle* composed of protein bands lying side by side, they can assume different shapes as the underlying cytoplasm undulates and contracts. As in certain other protists, there is a contractile vacuole for ridding the body of excess water. Euglenids reproduce by longitudinal cell division, and sexual reproduction is not known to occur.

Parabasalids and Diplomonads

Parabasalids and diplomonads are excavates that are single-celled, flagellated protozoans able to survive in environments with very low oxygen levels. This is because they lack mitochondria, and rely on fermentation for the production of ATP. They typically inhabit inner recesses of animal hosts.

Parabasalids have a fibrous connection between the Golgi apparatus and flagella. *Trichomonas vaginalis* is a sexually transmitted cause of vaginitis when it infects the vagina and urethra of women. The parasite may also infect the male genital tract; however, the male may have no symptoms.

A **diplomonad** [Gk. *diplo*, double, and *monas*, unit] cell has two nuclei and two sets of flagella. The diplomonad *Giardia lamblia* forms cysts that are transmitted by way of contaminated water and attach to the human intestinal wall, causing severe diarrhea (Fig. 21.19). Although *Giardia* is the most common flagellate of the human digestive tract, the protozoan lives in a variety of other mammals as well. Bea-

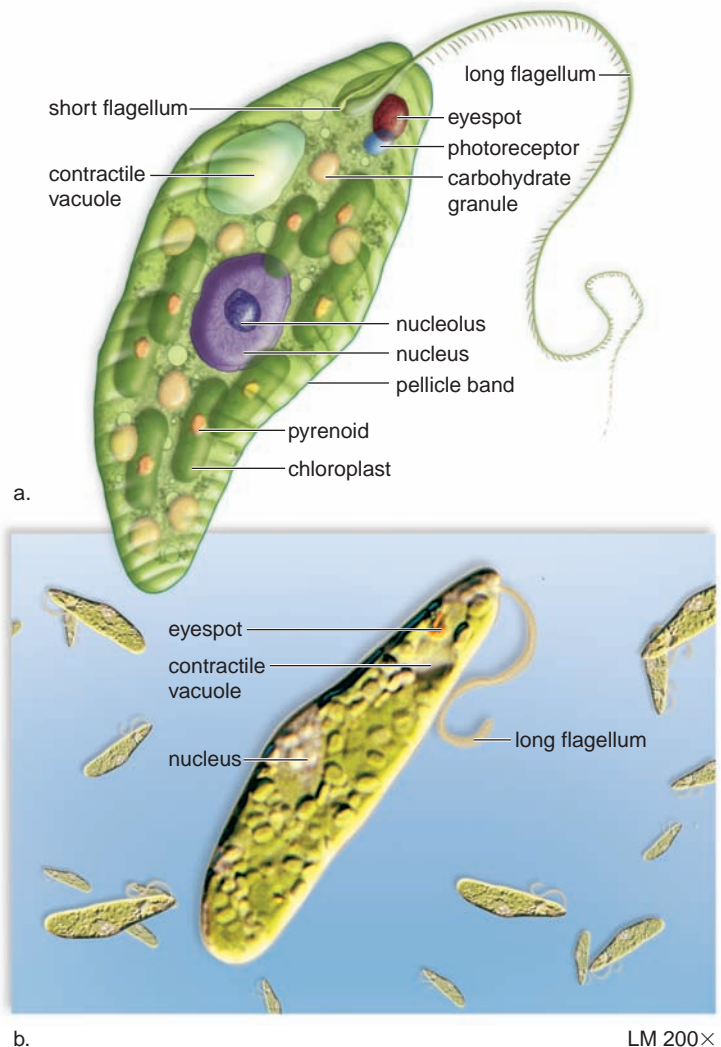


FIGURE 21.18 *Euglena*.

a. In *Euglena*, a very long flagellum propels the body, which is enveloped by a flexible pellicle. **b.** Micrograph of several specimens.

vers are known to be a reservoir of infection in the mountains of western United States, and many cases of infection have been acquired by hikers who fill their canteens at a beaver pond.

Kinetoplastids

The **kinetoplastids** are single-celled, flagellated protozoans named for their distinctive *kinetoplasts*, large masses of DNA found in their mitochondria. Trypanosomes are parasitic kinetoplastids that are passed to humans by insect bites. *Trypanosoma brucei*, transmitted by the bite of the tsetse fly, is the cause of African sleeping sickness (Fig. 21.20). The white blood cells in an infected human accumulate around the blood vessels leading to the brain and cut off circulation. The lethargy characteristic of the disease is caused by an inadequate supply of oxygen to the brain. Many thousands of cases are diagnosed each year. Fatalities or permanent brain damage are common. *Trypanosoma cruzi* causes Chagas

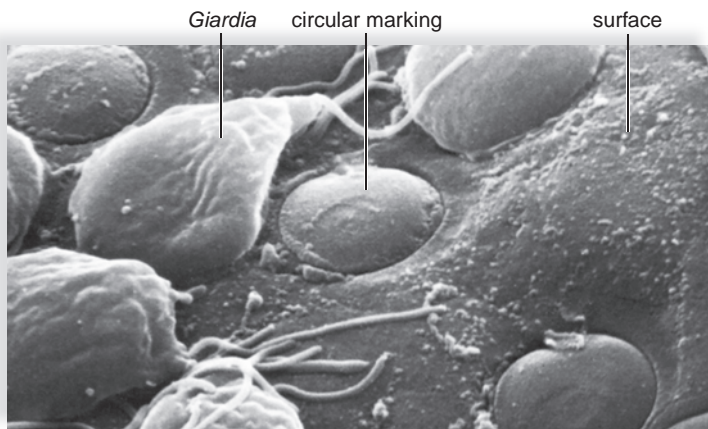


FIGURE 21.19 *Giardia lamblia*.

The protist adheres to any surface, including epithelial cells, by means of a sucking disk. Characteristic markings can be seen after the disk detaches.

disease in humans in Central and South America. Approximately 45,000 people die yearly from this parasite.

Check Your Progress

21.2D

1. Among the excavates studied, only *Euglena* is photosynthetic. How might you account for *Euglena* having chloroplasts?
2. What anatomical feature of the other excavates studied might make you think they were free-living?

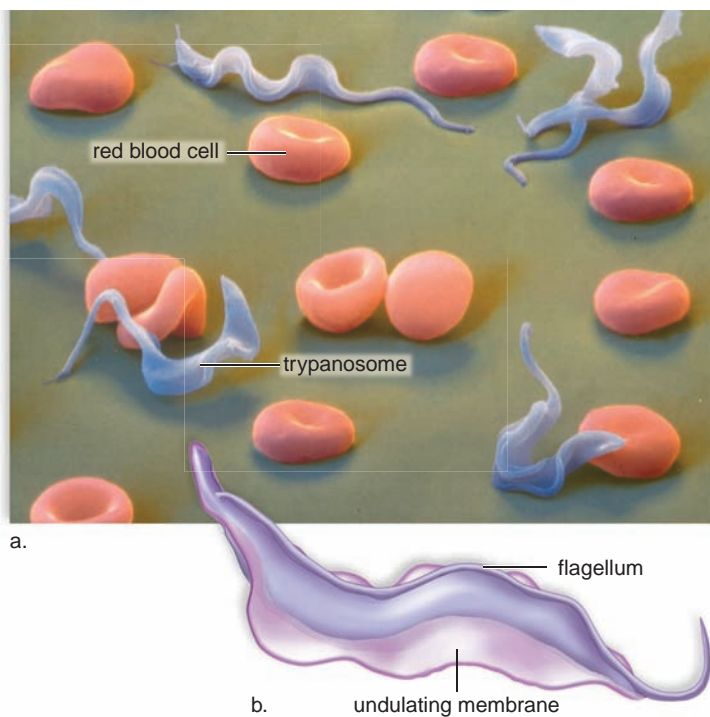


FIGURE 21.20 *Trypanosoma brucei*.

a. Micrograph of *Trypanosoma brucei*, a causal agent of African sleeping sickness, among red blood cells. **b.** The drawing shows its general structure.

Supergroup Amoebozoans

The **amoebozoans** [Gk. *ameibein*, to change, *zoa*, animal] is comprised of protozoans that move by **pseudopods** [Gk. *pseudes*, false, and *podos*, foot], processes that form when cytoplasm streams forward in a particular direction. Amoebozoans usually live in aquatic environments, in oceans and freshwater lakes and ponds, and they are often a part of the plankton.

Amoeboids

The **amoeboids** are protists that move and also ingest their food with pseudopods. Hundreds of species of amoeboids have been classified. *Amoeba proteus* is a commonly studied freshwater member of this group (Fig. 21.21). When amoeboids feed, the pseudopods surround and **phagocytize** [Gk. *phagein*, eat, and *kytos*, cell] their prey, which may be algae, bacteria, or other protists. Digestion then occurs within a **food vacuole**. Freshwater amoeboids, including *Amoeba proteus*, have **contractile vacuoles** where excess water from the cytoplasm collects before the vacuole appears to “contract,” releasing the water through a temporary opening in the plasma membrane.

Entamoeba histolytica is a parasitic amoeboid that lives in the human large intestine and causes amoebic dysentery. The ability of the organism to form cysts makes amoebic dysentery infectious. Complications arise when this parasite invades the intestinal lining and reproduces there. If the parasites enter the body proper, liver and brain involvement can be fatal.

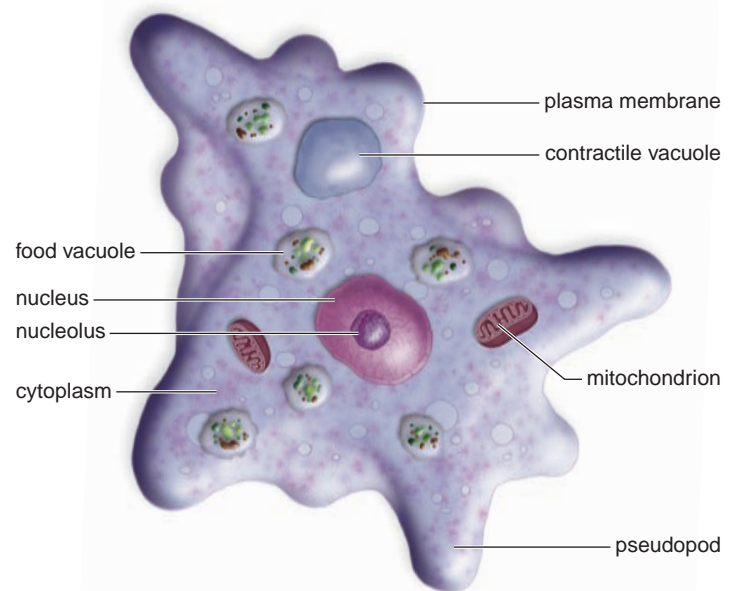


FIGURE 21.21 *Amoeba proteus*.

This amoeboid is common in freshwater ponds. Bacteria and other microorganisms are digested in food vacuoles, and contractile vacuoles rid the body of excess water.

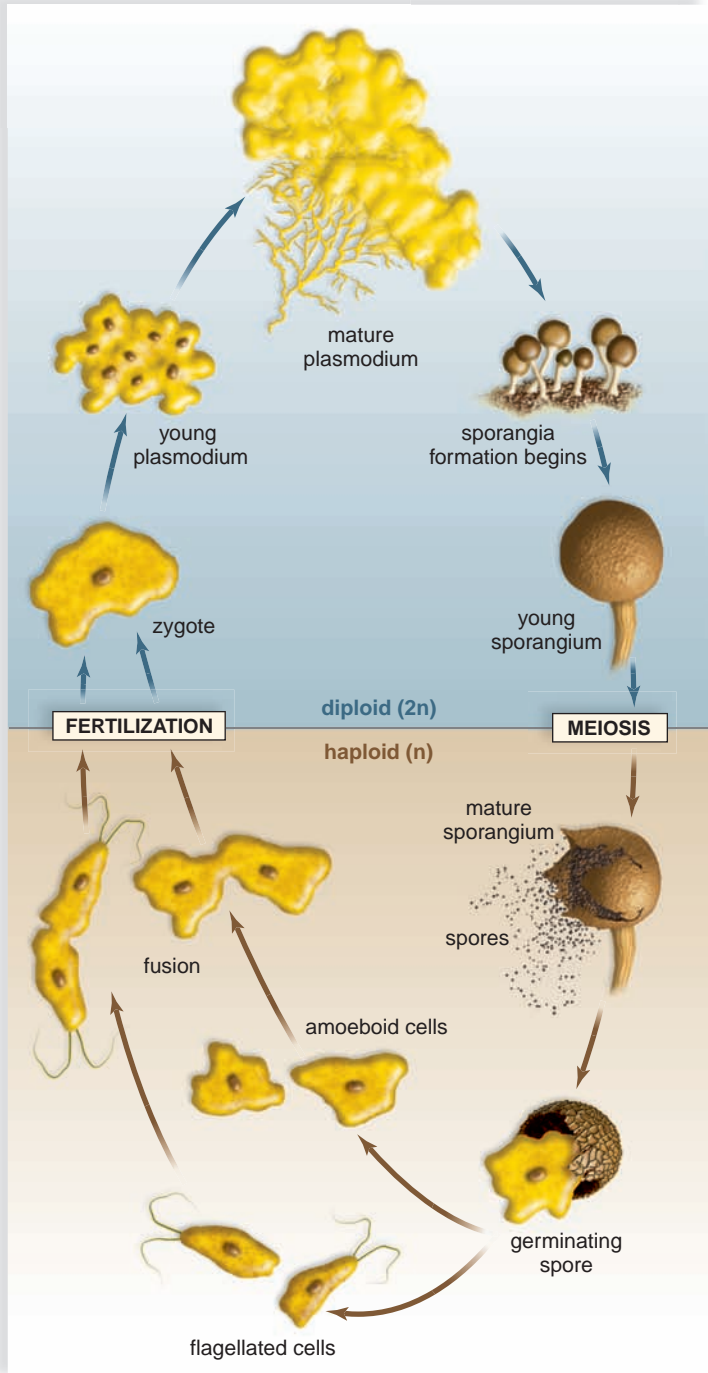
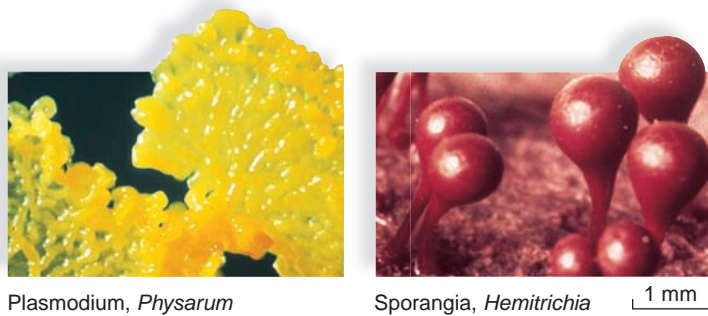


FIGURE 21.22 Plasmodial slime molds.

The diploid adult forms sporangia during sexual reproduction, when conditions are unfavorable to growth. Haploid spores germinate, releasing haploid amoeboid or flagellated cells that fuse.

Slime Molds

In forests and woodlands, slime molds contribute to ecological balance when they phagocytize, and therefore help dispose of, dead plant material. They also feed on bacteria, keeping their population under control. Slime molds were once classified as fungi, but unlike fungi, they lack cell walls, and have flagellated cells at some time during their life cycle. The vegetative state of the slime molds is mobile and amoeboid. Slime molds produce spores by meiosis; the spores germinate to form gametes.

Usually, **plasmodial slime molds** exist as a plasmodium, a diploid, multinucleated, cytoplasmic mass enveloped by a slime sheath that creeps along, phagocytizing decaying plant material in a forest or agricultural field (Fig. 21.22). Approximately 700 species of plasmodial slime molds have been described. Many species are brightly colored. At times unfavorable to growth, such as during a drought, the plasmodium develops many sporangia. A **sporangium** [Gk. *spora*, seed, and *angeion* (dim. of *angos*), vessel] is a reproductive structure that produces spores. An aggregate of sporangia is called a fruiting body.

The spores produced by a plasmodial slime mold sporangium can survive until moisture is sufficient for them to germinate. In plasmodial slime molds, spores release a haploid flagellated cell or an amoeboid cell. Eventually, two of them fuse to form a zygote that feeds and grows, producing a multinucleated plasmodium once again.

Cellular slime molds are called such because they exist as individual amoeboid cells. They are common in soil, where they feed on bacteria and yeasts. Their small size prevents them from being seen. Nearly 70 species of cellular slime molds have been described.

As the food supply runs out or unfavorable environmental conditions develop, the cells release a chemical that causes them to aggregate into a pseudoplasmodium. The pseudoplasmodium stage is temporary and eventually gives rise to a fruiting body in which sporangia produce spores. When favorable conditions return, the spores germinate, releasing haploid amoeboid cells, and the asexual cycle begins again.

Supergroup Opisthokonts

Animals and fungi are included in supergroup **opisthokonts** (op is thoe KONTs) [Gk. *opisthos*, behind, *kontos*, pole] along with several closely related protists. This supergroup includes both unicellular and multicellular protozoans. Among the opisthokonts are the **choanoflagellates**, animal-like protozoans that are near relatives of sponges. The choanoflagellates, including unicellular as well as colonial forms, are filter-feeders with cells that bear a striking resemblance to the feeding cells of sponges, called choanocytes (see page 523). The cells each have a single posterior flagellum surrounded by a collar of slender microvilli. Beating of the flagellum creates a water current that flows through the collar, where food particles are taken in by phagocytosis. Colonial choanoflagellates such as *Codonosiga* (Fig. 21.23a) commonly attach to surfaces with a stalk, but sometimes float freely like *Proterospongia* (Fig. 21.23b).

Nucleariids are opisthokonts with a rounded or slightly flattened cell body and threadlike pseudopods called filopodia.



Most feed on algae or cyanobacteria. Although they lack the characteristic cell walls found in fungi, nucleariids appear to be close fungal relatives due to molecular similarities.

Supergroup Rhizarians

The **rhizarians** [Gk. *rhiza*, root] consist of the **foraminiferans** and the **radiolarians**, organisms with fine, threadlike pseudopods. Although they were previously classified along with amoebozoans, the rhizarians are now assigned to a different supergroup because molecular data indicate the two groups are not very closely related. Foraminiferans and radiolarians both have a skeleton called a **test**. The tests of foraminiferans and radiolarians are intriguing and beautiful. In the foraminiferans, the calcium carbonate test is often multichambered. The pseudopods extend through openings in the test, which covers the plasma membrane (Fig. 21.24a). In the radiolarians, the glassy silicon test is internal and usually has a radial arrangement of spines (Fig. 21.24b). The pseudopods are external to the test.

The tests of dead foraminiferans and radiolarians form a deep layer (700–4,000 m) of sediment on the ocean floor. The radiolarians lie deeper than the foraminiferans because their glassy test is insoluble at greater pressures. The presence of either or both is used as an indicator of oil deposits on land and sea. Their fossils date even as far back as to Precambrian times and are evidence of the antiquity of the protists. Because each geological period has a distinctive form of foraminiferan, they can be used as index fossils to

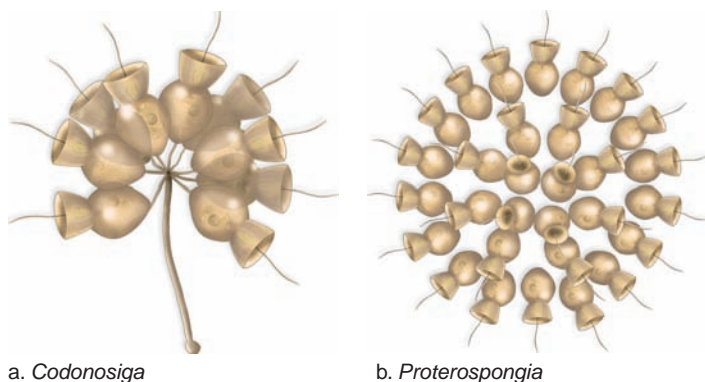


FIGURE 21.23 Colonial choanoflagellates.

a. A *Codonosiga* colony can anchor itself with a slender stalk. **b.** A *Proterospongia* colony is unattached.

date sedimentary rock. Deposits of foraminiferans for millions of years, followed by geological upheaval, formed the White Cliffs of Dover along the southern coast of England. Also, the great Egyptian pyramids are built of foraminiferan limestone. One foraminiferan test found in the pyramids is about the size of a silver dollar. This species, known as *Nummulites*, has been found in deposits worldwide, including central eastern Mississippi. The shells of foraminiferans and radiolarians are abundant in the ocean.

Check Your Progress

21.2E

1. How do the opisthokonts differ from the amoebozoans and the rhizarians?
2. What link is visual evidence between animals and the opisthokonts?



a. Foraminiferan, *Globigerina*, and the White Cliffs of Dover, England



b. Radiolarian tests

SEM 200×

FIGURE 21.24 Foraminiferans and radiolarians.

a. Pseudopods of a live foraminiferan project through holes in the calcium carbonate shell. Fossilized shells were so numerous they became a large part of the White Cliffs of Dover when a geological upheaval occurred. **b.** Skeletal test of a radiolarian. In life, pseudopods extend outward through the openings of the glassy silicon shell.

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Connecting the Concepts

It's possible that the origin of sexual reproduction played a role in fostering the diversity of protists and their ability to inhabit water, soil, food, and even air. Unicellular *Chlamydomonas* usually reproduces asexually, but when it does reproduce sexually, the gametes look alike. Colonial forms of algae, such as *Volvox*, and multicellular forms, such as the brown alga *Fucus*, have a more specialized form of gametogenesis. They undergo oogamy: One gamete is larger and immobile, and the other is flagellated and motile. The green alga *Ulva* and the foraminiferans have an alternation of

generations life cycle in which only the haploid stage produces gametes.

Conjugation is another way to introduce genetic variation among offspring. *Spirogyra* undergoes conjugation, but the ciliates have taken conjugation to another level. In ciliates, one haploid nucleus in each mating cell survives meiosis and divides again by mitosis. An exchange of haploid nuclei through a cytoplasmic channel restores diploidy and ensures diversity of genes.

Reproduction in protists is adaptive in still another way. As a part of their life cycle, some

protists form spores or cysts that can survive in a hostile environment. The cell emerging from a spore or cyst is often a re-formed haploid or diploid individual, depending on the protist. Spores and cysts can survive inclement conditions for years on end.

The diversity of reproduction among protists exemplifies why it is difficult to discover their evolutionary relationships to the fungi, land plants, and animals without molecular genetics, which can detect evolutionary relationships by using nucleotide sequences.

summary

21.1 General Biology of Protists

Protists are in the domain Eukarya. Independent endosymbiotic events may account for the presence of mitochondria and chloroplasts in eukaryotic cells. Protists are generally unicellular, but still they are quite complex because they (1) have a variety of characteristics, (2) acquire nutrients in a number of ways, and (3) have complicated life cycles that include the ability to withstand hostile environments.

Protists are of great ecological importance because in largely aquatic environments they are the producers that support communities of organisms. Protists also enter into various types of symbiotic relationships. Their great diversity makes it difficult to classify protists, and as yet, there is no general agreement about their categorization. In this chapter, they have been arranged in six supergroups.

21.2 Diversity of Protists

The archaeplastids include the plants and all green and red algae. Green algae possess chlorophylls *a* and *b*, store reserve food as starch, and have cell walls of cellulose as do land plants. Green algae are divided into chlorophytes and charophytes. Chlorophytes include forms that are unicellular (*Chlamydomonas*), colonial (*Volvox*), and multicellular (*Ulva*). Charophytes include filamentous forms (*Spirogyra*), as well as the stoneworts (*Chara*) and are thought to be the closest living relatives of land plants. The life cycle varies among the green algae. In most, the zygote undergoes meiosis, and the adult is haploid. *Ulva* has an alternation of generations like land plants, but the sporophyte and gametophyte generations are similar in appearance; the gametes look alike. Red algae are filamentous or multicellular seaweeds that are more delicate than brown algae and are usually found in warmer waters. Red algae have notable economic importance.

The supergroup chromalveolates consists of stramenopiles such as brown algae, diatoms, golden brown algae, and water molds; and alveolates, including dinoflagellates, ciliates, and apicomplexans. Brown algae have chlorophylls *a* and *c* plus a brownish carotenoid pigment. The large, complex brown algae,

commonly called seaweeds, are well known and economically important. Diatoms, which have an outer layer of silica, are extremely numerous in both marine and freshwater ecosystems, as are golden brown algae, which may have coverings of silica or organic material. Water molds, which are filamentous and heterotrophic by absorption, are unlike fungi in that they produce flagellated 2n zoospores. Dinoflagellates usually have cellulose plates and two flagella, one at a right angle to the other. They are extremely numerous in the ocean and, on occasion, produce a neurotoxin when they form red tides. The ciliates move by their many cilia. They are remarkably diverse in form, and as exemplified by *Paramecium*, they show how complex a protist can be despite being a single cell. The apicomplexans are nonmotile parasites that form spores; *Plasmodium* causes malaria.

Supergroup excavates is a diverse collection of single-celled, motile protists, including euglenids, parabasalids, diplomonads, and kinetoplastids. Euglenids are flagellated cells with a pellicle instead of a cell wall. Their chloroplasts are most likely derived from a green alga through endosymbiosis. Many of the kinetoplastids are parasites, including trypanosomes, such as those that cause Chagas disease and African sleeping sickness in humans. Parabasalids, such as *Trichomonas vaginalis*, and, diplomonads, such as *Giardia lamblia*, are common inhabitants of animal hosts. They thrive in low-oxygen conditions due to their lack of aerobic respiration.

The amoebozoans supergroup contains amoeboids and slime molds, protists that use pseudopods for motility and feeding. Amoeboids move and feed by forming pseudopods. In *Amoeba proteus*, food vacuoles form following phagocytosis of prey. Contractile vacuoles discharge excess water. Slime molds, which produce nonmotile spores, are unlike fungi in that they have an amoeboid stage and are heterotrophic by ingestion.

The opisthokonts supergroup includes kingdom Animalia, the animal-like protists known as choanoflagellates, kingdom Fungi, and the funguslike protists called nucleariids.

The rhizarians are a supergroup that includes the foraminiferans and radiolarians, protists with threadlike pseudopods and skeletons called tests. The tests of foraminiferans and radiolarians form a deep layer of sediment on the ocean floor. The tests of foraminiferans are responsible for the limestone deposits of the White Cliffs of Dover.

understanding the terms

algae 374	green algae 377
alveolate 383	kinetoplastid 386
amoeboid 387	mixotrophic 374
amoebozoan 387	nucleariid 388
apicomplexan 384	opisthokont 388
archaeplastid 377	parabasalid 386
brown algae 381	phagocytize 387
cellular slime mold 388	plankton 374
charophyte 377	plasmodial slime mold 388
chlorophyte 377	protist 374
choanoflagellate 388	protozoan 374
chromalveolate 381	pseudopod 387
ciliate 384	radiolarian 389
colony 378	red algae 379
conjugation 378	red tide 383
cyst 374	rhizarian 389
diatom 382	sporangium 388
dinoflagellate 383	stramenopile 381
diplomonad 386	supergroup 374
euglenid 386	test 388
excavate 386	trichocyst 384
filament 378	water mold 382
foraminiferan 389	zooflagellate 386
golden brown algae 382	zoospore 377

Match the terms to these definitions:

- _____ Cytoplasmic extension of amoeboid protists; used for locomotion and engulfing food.
- _____ Flexible freshwater unicellular organism that usually contains chloroplasts and is flagellated.
- _____ Freshwater or marine unicellular protist with a cell wall consisting of two silica-impregnated valves; extremely numerous in phytoplankton.
- _____ Causes severe diseases in human beings and domestic animals, including a condition called sleeping sickness.
- _____ Freshwater and marine organisms that are suspended on or near the surface of the water.

reviewing this chapter

- List and discuss ways that protists are varied. 374
- Describe the structures of *Chlamydomonas* and *Volvox*, and contrast how they reproduce. 377–78
- Describe the structures of *Ulva* and *Spirogyra*, and explain how they reproduce. 378
- Describe the structure of red algae, and discuss their economic importance. 379
- Describe the structure of brown algae, and discuss their ecological and economic importance. 381
- Describe the structures of diatoms and dinoflagellates. What is a red tide? 382–84
- Describe the life cycle of *Plasmodium vivax*, the most common causative agent of malaria. 385
- Describe the unique structure of euglenids. 386
- How are ciliates like and different from amoeboids? 384–85, 387–88
- What features distinguish slime molds and water molds from fungi? Describe the life cycle of a plasmodial slime mold. 383, 388

- Distinguish between amoeboids, foraminiferans, and radiolarians. 387–89

testing yourself

Choose the best answer for each question.

For questions 1–6, match each item to those in the key.

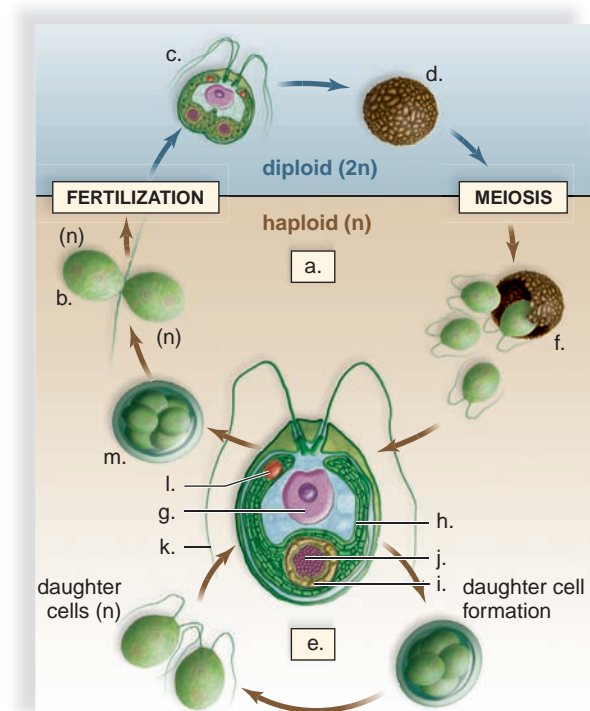
KEY:

- | | |
|--------------------|-----------------|
| a. Amoebozoans | d. Excavates |
| b. Archaeplastids | e. Opisthokonts |
| c. Chromalveolates | f. Rhizarians |

- foraminiferans
- ciliates
- brown algae
- amoeboids
- green algae
- choanoflagellates
- Which of these is not a green alga?
 - Volvox*
 - Fucus*
 - Spirogyra*
 - Chlamydomonas*
 - Ulva*
- Which is not a characteristic of brown algae?
 - multicellular
 - chlorophylls *a* and *b*
 - live along rocky coast
 - harvested for commercial reasons
 - contain a brown pigment
- In *Chlamydomonas*,
 - the adult is haploid.
 - the zygospore survives times of stress.
 - sexual reproduction occurs.
 - asexual reproduction occurs.
 - All of these are correct.
- Ulva*
 - undergoes alternation of generations.
 - is sea lettuce.
 - is multicellular.
 - is an archaeplastid.
 - All of these are correct.
- Which of these protists are not flagellated?
 - Volvox*
 - Spirogyra*
 - dinoflagellates
 - Chlamydomonas*
 - trypanosomes
- Which pair is mismatched?
 - diatoms—silica shell, resemble a petri dish, free-living
 - euglenids—flagella, pellicle, eyespot
 - Fucus*—adult is diploid, seaweed, chlorophylls *a* and *c*
 - Paramecium*—cilia, calcium carbonate shell, gullet
 - foraminiferan—test, pseudopod, digestive vacuole
- Which is a false statement?
 - Only heterotrophic and not photosynthetic protists are flagellated.
 - Apicomplexans are parasitic protozoans.
 - Among protists, the haploid cycle is common.
 - Ciliates exchange genetic material during conjugation.
 - Slime molds have an amoeboid stage.

14. Which pair is mismatched?
- trypanosome—African sleeping sickness
 - Plasmodium vivax*—malaria
 - amoeboid—severe diarrhea
 - AIDS—*Giardia lamblia*
 - dinoflagellates—coral
15. Which is found in slime molds but not in fungi?
- nonmotile spores
 - flagellated cells
 - zygote formation
 - photosynthesis
 - chitin in cell walls
16. Which is a false statement?
- Slime molds and water molds are protists.
 - There are flagellated algae and flagellated protozoans.
 - Among protists, some flagellates are photosynthetic.
 - Among protists, only green algae ever have a sexual life cycle.
 - Conjugation occurs among green algae.
17. Which pair is properly matched?
- water mold—flagellate
 - trypanosome—zooflagellate
 - Plasmodium vivax*—mold
 - amoeboid—algae
 - golden brown algae—kelp
18. Which is an incorrect statement?
- Unicellular protists can be quite complex.
 - Euglenids are motile but have chloroplasts.
 - Plasmodial slime molds are amoeboid but have sporangia.
 - Volvox* is colonial but has a boxed shape.
 - Both b and d are incorrect.
19. All are correct about brown algae except that they
- range in size from small to large.
 - are a type of seaweed.
 - live on land.
 - are photosynthetic.
 - are usually multicellular.
20. In the haploid life cycle (e.g., *Chlamydomonas*),
- meiosis occurs following zygote formation.
 - the adult is diploid.
 - fertilization is delayed beyond the diploid stage.
 - the zygote produces sperm and eggs.
21. Dinoflagellates
- usually reproduce sexually.
 - have protective cellulose plates.
 - are insignificant producers of food and oxygen.
 - have cilia instead of flagella.
 - tend to be larger than brown algae.
22. Ciliates
- move by pseudopods.
 - are not as varied as other protists.
 - have a gullet for food gathering.
 - do not divide by binary fission.
 - are closely related to the radiolarians.
23. A(n) _____ is a collared, flagellated, heterotrophic protist that is closely related to animals such as sponges.
- radiolarian
 - kinetoplastid
 - choanoflagellate
 - amoeboid
 - trypanosome

24. Label this diagram of the *Chlamydomonas* life cycle.



thinking scientifically

- While studying a unicellular alga, you discover a mutant in which the daughter cells do not separate after mitosis. This gives you an idea about how filamentous algae may have evolved. You hypothesize that the mutant alga is missing a protein or making a new form of a protein. How might each possibly lead to a filamentous appearance?
- You are trying to develop a new antitermite chemical that will not harm environmentally beneficial insects. Since termites are adapted to eat only wood, they will starve if they cannot digest this food source. Termites have two symbiotic partners: the protozoan *Trichonympha collaris* and the bacteria it harbors that actually produce the enzyme that digests the wood. Knowing this, how might you prevent termite infestations without targeting the termites directly?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

<http://www.mhhe.com/maderbiology10>

22

Fungi Evolution and Diversity

the largest living organism known is a honey mushroom, whose meshlike body spreads underground for 2,200 acres in the Blue Mountains of eastern Oregon. The reproductive structures of mushrooms and other fungi, such as puffballs, morels, and truffles, appear above ground only occasionally. Most of the time, fungi are busy decomposing leaf litter, fallen tree trunks, and the carcasses of dead animals. It's even been said that without the ability of fungi to coat and help plant roots take up nutrients, plants would not have been able to invade land. Some symbiotic fungi, however, cause diseases in plants and animals, including athlete's foot and ringworm in humans. Still, humans have found many uses for fungi. They are a food source and they help us produce beer, wine, bread, and cheeses.

Fungi were once classified as plants, because they have a cell wall and their bodies are nonmotile. However, molecular data now indicate that fungi are much more closely related to animals than they are to plants. Like animals, fungi are heterotrophs. Unlike animals, which ingest and then digest their food, fungi digest their food externally and then absorb the nutrients. In this chapter, you will explore the characteristics and sample the diversity of kingdom Fungi.

Honey mushroom, *Armillaria ostoyae*, a common cause of tree root rot in the northeastern United States and British Columbia (Canada).



22.1 EVOLUTION AND CHARACTERISTICS OF FUNGI

- Fungi are saprotrophic decomposers that aid the cycling of inorganic nutrients in ecosystems. The body of most fungi is multicellular; it is composed of thin filaments called hyphae. 394–95

22.2 DIVERSITY OF FUNGI

- Five widely recognized groups of fungi are chytrids, zygosporangia, AM fungi, sac fungi, and club fungi. 396–403
- Chytrids are the only group of aquatic fungi; the other groups are adapted to living on land particularly by producing windblown spores during both asexual and sexual life cycles. 396–403
- The terrestrial fungi impact the lives of both plants and animals, including humans. 396–403

22.3 SYMBIOTIC RELATIONSHIPS OF FUNGI

- Lichens are an association between a fungus and a cyanobacterium or a green alga. Mycorrhizae are an association between a fungus and the roots of a plant. 404–5

22.1 Evolution and Characteristics of Fungi

The **fungi** include over 80,000 species of mostly multicellular eukaryotes that share a common mode of nutrition. Mycologists, scientists that study fungi, expect this number of species to increase to over 1.5 million in the future. Like animals, fungi are heterotrophic and consume preformed organic matter. Animals, however, are heterotrophs that ingest food, while fungi are **saprotrophs** that absorb food. Their cells send out digestive enzymes into the immediate environment and then, when organic matter is broken down, the cells absorb the resulting nutrient molecules.

Evolution of Fungi

Figure 22.1 lists the groups of fungi we will be discussing and some of the criteria used to distinguish each group. The evolutionary tree shows how these groups are believed to be related. As you can see, the chytrids are different from all other fungi because they are aquatic and have flagellated spores and gametes. Our description of fungal structure applies best to the zygosporangium fungi, sac fungi, and the club fungi. The AM fungi exist only as mycorrhizae in association with plant roots!

Protists evolved some 1,500 MYA (million years ago). Plants, animals, and fungi can all trace their ancestry to protists, but molecular data tells that animals and fungi shared a common ancestor after plants evolved. Therefore, animals and fungi are more closely related to each other than either is to plants. The common ancestor of animals and fungi was most likely a flagellated unicellular protist, and each became multicellular sometime after they split from one another. The ancestor was also aquatic and flagellated. Animals have retained flagellated cells but most groups of fungi do not have flagella today.

Fungal anatomy doesn't lend itself to becoming fossilized, so fungi probably evolved a lot earlier than the earliest known fungal fossil dated 450 MYA. We do know that while animals were still swimming in the seas during the Silurian, plants were beginning to live on the land, and they brought fungi with them. Mycorrhizae are evident in plant fossils, also some 450 MYA. Perhaps fungi were instrumental in the colonization of land by plants. Much of the fungal diversity we observed most likely had its origin in an adaptive radiation when organisms began to colonize land.

Structure of Fungi

Some fungi, including the yeasts, are unicellular; however, the vast majority of species are multicellular. The thallus or body of most fungi is a multicellular structure known as a mycelium (Fig. 22.2a). A **mycelium** [Gk. *mycelium*, fungus filaments] is a network of filaments called **hyphae** [Gk. *hyphe*, web]. Hyphae give the mycelium quite a large surface area per volume of cytoplasm, and this facilitates absorption of nutrients into the body of a fungus. Hyphae grow at their tips, and the mycelium absorbs and then passes nutrients on to the growing tips. When a fungus reproduces, a specific portion of

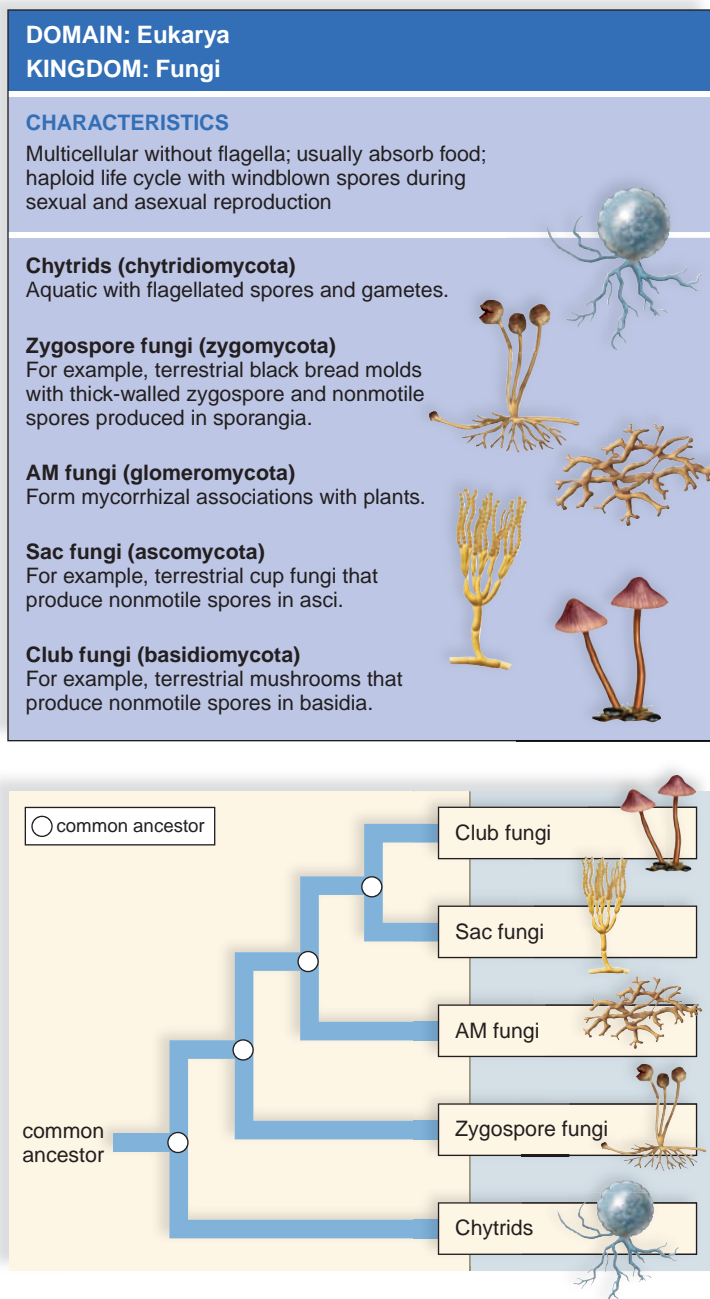


FIGURE 22.1 Evolutionary relationships among the fungi.

The common ancestor for the fungi was a flagellated saprotroph with chitin in the cell walls. All but chytrids lost the flagella at some point. They also became multicellular. Only the AM, sac, and club fungi are monophyletic, as is necessary to be a clade.

the mycelium becomes a reproductive structure that is then nourished by the rest of the mycelium (Fig. 22.2b).

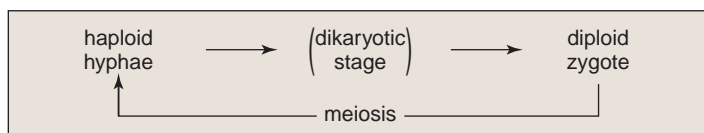
Fungal cells are quite different from plant cells, not only by lacking chloroplasts but also by having a cell wall that contains **chitin** and not cellulose. Chitin, like cellulose, is a polymer of glucose organized into microfibrils. In chitin, however, each glucose molecule has a nitrogen-containing amino group attached to it. Chitin is also found in the exoskeleton of arthropods, a major phylum of animals that includes the insects and crustaceans. The energy reserve of fungi is not starch but glycogen, as in animals.

Except for the aquatic chytrids (discussed on page 396), fungi lack motility. The terrestrial fungi lack basal bodies and do not have flagella at any stage in their life cycle. They move toward a food source by growing toward it. Hyphae can cover as much as a kilometer a day!

Some fungi have cross walls, or septa, in their hyphae. These hyphae are called **septate** [L. *septum*, fence, wall]. Actually, the presence of septa makes little difference because pores allow cytoplasm and sometimes even organelles to pass freely from one cell to the other. The septa that separate reproductive cells, however, are complete in all fungal groups. **Nonseptate** fungi are multinucleated; they have many nuclei in the cytoplasm of a hypha (Fig. 22.2c).

Reproduction of Fungi

Both sexual and asexual reproduction occur in fungi. Terrestrial fungal sexual reproduction involves these stages:



The relative length of time of each phase varies with the species.

During sexual reproduction, hyphae (or a portion thereof) from two different mating types make contact and fuse. It would be expected that the nuclei from the two mating types would also fuse immediately, and they do in some species. In other species, the nuclei pair but do not fuse for days, months, or even years. The nuclei continue to divide in such a way that every cell (in septate hyphae) has at least one of each nucleus. A hypha that contains paired haploid nuclei is said to be $n + n$ or **dikaryotic** [Gk. *dis*, two, and *karyon*, nucleus, kernel]. When the nuclei do eventually fuse, the zygote undergoes meiosis prior to spore formation. Fungal spores germinate directly into haploid hyphae without any noticeable embryological development.

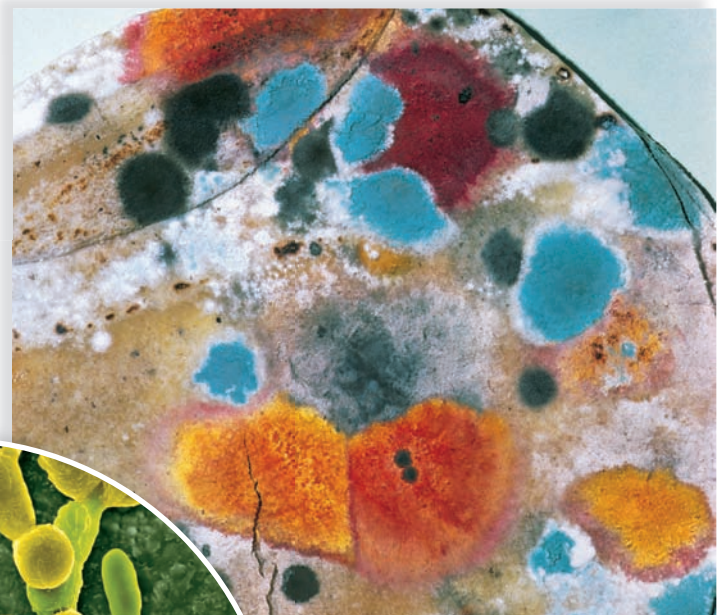
How can the terrestrial and nonmotile fungi ensure that the offspring will be dispersed to new locations? As an adaptation to life on land, fungi usually produce nonmotile, but normally windblown, spores during both sexual and asexual reproduction. A **spore** is a reproductive cell that develops into a new organism without the need to fuse with another reproductive cell. A large mushroom may produce billions of spores within a few days. When a spore lands upon an appropriate food source, it germinates and begins to grow.

Asexual reproduction usually involves the production of spores by a specialized part of a single mycelium. Alternately, asexual reproduction can occur by fragmentation—a portion of a mycelium begins a life of its own. Also, unicellular yeasts reproduce asexually by **budding**; a small cell forms and gets pinched off as it grows to full size (see Fig. 22.5).

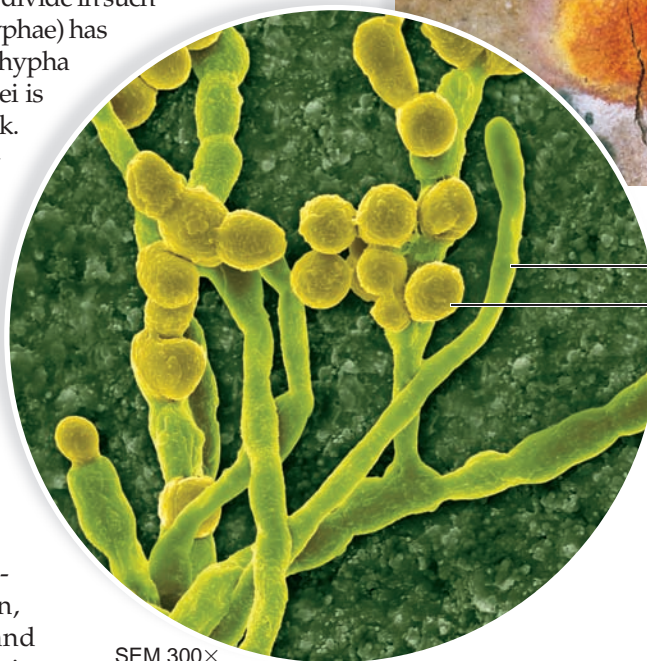
Check Your Progress

22.1

1. How do animals and fungi differ with respect to heterotrophy?
2. How are fungal cell walls different from plant cell walls?
3. Describe the function of a fungal spore.

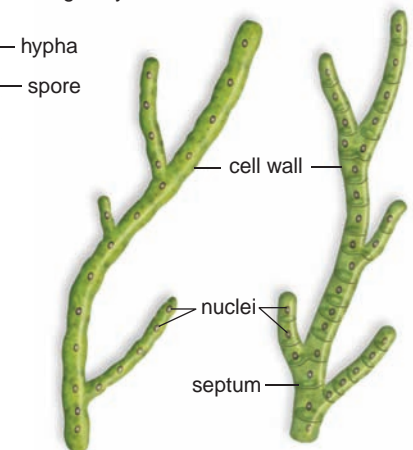


a. Fungal mycelia on a corn tortilla



SEM 300×

b. Specialized fungal hyphae that bear spores



c. nonseptate hypha

septate hypha

FIGURE 22.2 Mycelia and hyphae of fungi.

a. Each mycelium grown from a different spore on a corn tortilla is quite symmetrical. b. Scanning electron micrograph of specialized aerial fungal hyphae that bear spores. c. Hyphae are either nonseptate (do not have cross walls) or septate (have cross walls).

22.2 Diversity of Fungi

R. H. Whittaker was the first to say, in 1969, that fungi should be classified as a separate group from protists, plants, and animals, and they remain so today. He based his reasoning on the observation that fungi are the only type of multicellular organism to be saprotrophic. However, as discussed in the previous chapter, some experts now place fungi in the supergroup opisthokonts, which includes animals and certain heterotrophic protists (see page 389).

Without an adequate fossil record, we cannot be certain about the relationship between different types of fungi. However, with the ever more common use of comparative molecular data to decipher evolutionary relationships, we may one day know how the fungi are related. In the meantime, the fungal groups chytrids, zygospor fungi, AM fungi, sac fungi, and club fungi are differentiated according to their life cycle and the type of structure they use to produce spores.

Chytrids

The **chytrids** (chytridiomycota) include about 790 species of the simplest fungi that may resemble the first fungi to have evolved. Some chytrids are single cells; others form branched nonseptate hyphae. Chytrids are unique among fungi because they are the only fungi to still have flagellated cells. This feature is consistent with their aquatic lifestyle, although some also live in moist soil. They produce flagellated gametes and spores. The placement of the flagella in their spores, called **zoospores**, links fungi to choanoflagellates and animals and helps place fungi in the supergroup opisthokonts (see page 389). Most chytrids reproduce asexually through the production of zoospores within a single cell. The zoospores grow into new chytrids. However, some have an alternation of generations life cycle, much like that

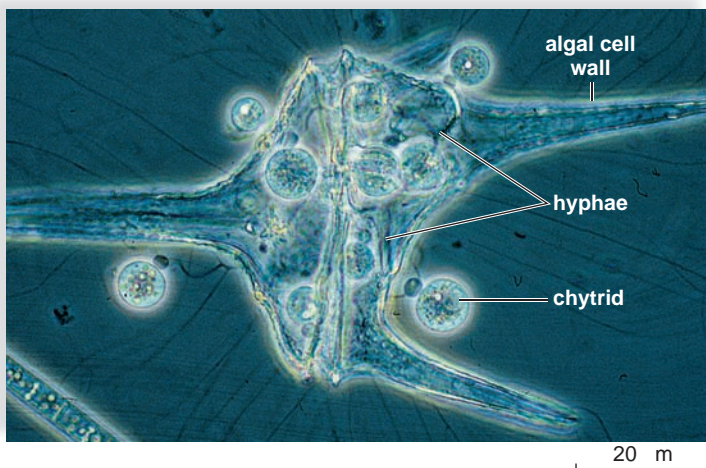


FIGURE 22.3 Chytrids parasitizing a protist.

These aquatic chytrids (*Chytridiomycetes hyalinus*) have penetrated the cell walls of this dinoflagellate and are absorbing nutrients meant for their host. They will produce flagellated zoospores that will go on to parasitize other protists.

of green plants and certain algae, which is quite uncommon among fungi.

Most chytrids play a role in the decay and digestion of dead aquatic organisms, but some are parasitic on plants, animals, and protists (Fig. 22.3). They are also known to cause diseases such as brown spot of corn and black wart of potato. The parasitic chytrid *Batrachochytrium dendrobatidis* has recently decimated populations of harlequin frogs (*Atelopus*) in Central and South America. They grow inside skin cells and disrupt the ability of frogs to acquire oxygen through their skin.

Zygospor Fungi

The **zygospor fungi** (zygomycota) include approximately 1,050 species of fungi. These organisms are saprotrophic, living off plant and animal remains in the soil or in bakery goods in the pantry. Some are parasites of minute soil protists, worms, and insects such as a housefly.

The black bread mold, *Rhizopus stolonifer*, is commonly used as an example of this phylum. The body of this fungus, which is composed of mostly nonseptate hyphae, demonstrates that although there is little cellular differentiation among fungi, the hyphae may be specialized for various purposes. In *Rhizopus*, stolons are horizontal hyphae that exist on the surface of the bread; rhizoids grow into the bread, anchor the mycelium, and carry out digestion; and sporangioophores are aerial hyphae that bear sporangia. A **sporangium** is a capsule that produces spores called sporangiospores. During asexual reproduction, all structures involved are haploid (Fig. 22.4).

The phylum name refers to the zygospor, which is seen during sexual reproduction. The hyphae of opposite mating types, termed plus (+) and minus (−), are chemically attracted, and they grow toward each other until they touch. The ends of the hyphae swell as nuclei enter; then cross walls develop a short distance behind each end, forming **gametangia**. The gametangia merge, and the result is a large multinucleate cell in which the nuclei of the two mating types pair and then fuse. A thick wall develops around the cell, which is now called a **zygospor**. The zygospor undergoes a period of dormancy before meiosis and germination take place. One or more sporangioophores with sporangia at their tips develop, and many spores are released. The spores, dispersed by air currents, give rise to new haploid mycelia. Spores from black bread mold have been found in the air above the North Pole, in the jungle, and far out at sea.

AM Fungi

The **AM fungi** (glomeromycota) are a relatively small group (160 species) of fungi whose common name stands for arbuscular mycorrhizal fungi. Arbuscules are branching invaginations that the fungus makes when it invades plant roots. Mycorrhizae, which are discussed on page 404, are a mutualistic association that benefit both the fungus and the plant. Long classified as zygospor fungi, the AM fungi are now beginning to receive recognition as a separate group based on molecular data.