

13 | DIVERSITY OF MICROBES, FUNGI, AND PROTISTS

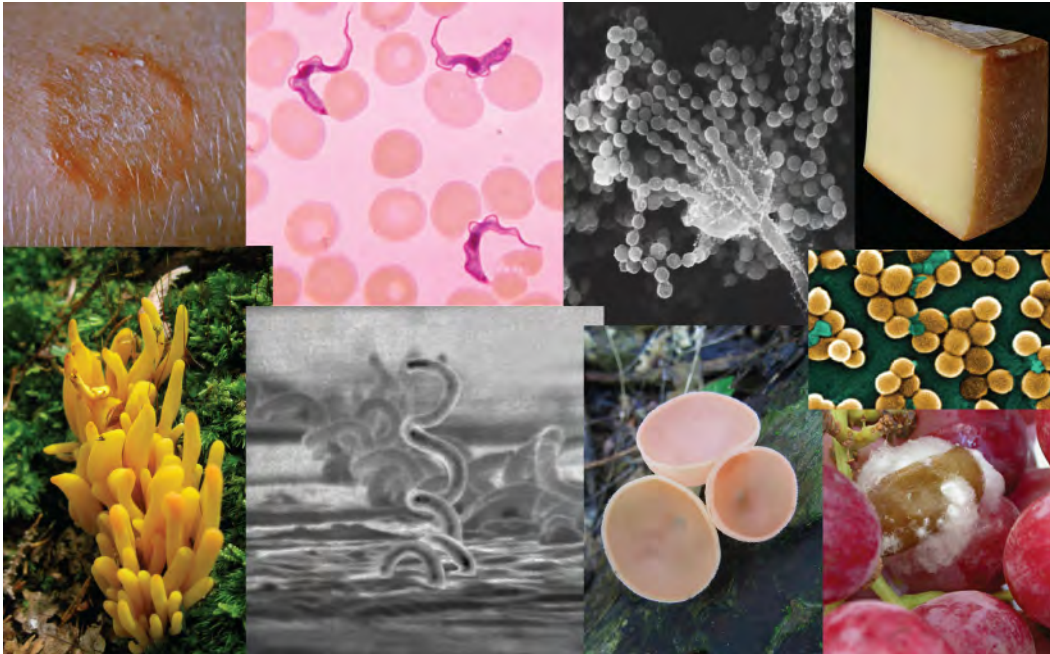


Figure 13.1 Living things are very diverse, from simple, single-celled bacteria to complex, multicellular organisms. (credit "ringworm": modification of work by Dr. Lucille K. Georg, CDC; credit "Trypanosomes": modification of work by Dr. Myron G. Schultz, CDC; credit "tree mold": modification of work by Janice Haney Carr, Robert Simmons, CDC; credit "coral fungus": modification of work by Cory Zanker; credit "bacterium": modification of work by Dr. David Cox, CDC; credit "cup fungus": modification of work by "icelight"/Flickr; credit "MRSA": modification of work by Janice Haney Carr, CDC; credit "moldy grapefruit": modification of work by Joseph Smilanick)

Chapter Outline

- 13.1: Prokaryotic Diversity**
- 13.2: Eukaryotic Origins**
- 13.3: Protists**
- 13.4: Fungi**

Introduction

Until the late twentieth century, scientists most commonly grouped living things into five kingdoms—animals, plants, fungi, protists, and bacteria—based on several criteria, such as absence or presence of a nucleus and other membrane-bound organelles, absence or presence of cell walls, multicellularity, and mode of nutrition. In the late twentieth century, the pioneering work of Carl Woese and others compared nucleotide sequences of small-subunit ribosomal RNA (SSU rRNA), which resulted in a dramatically different way to group organisms on Earth. Based on differences in the structure of cell membranes and in rRNA, Woese and his colleagues proposed that all life on Earth evolved along three lineages, called domains. The three domains are called Bacteria, Archaea, and Eukarya.

Two of the three domains—Bacteria and Archaea—are prokaryotic, meaning that they lack both a nucleus and true membrane-bound organelles. However, they are now considered, on the basis of membrane structure and rRNA, to be as different from each other as they are from the third domain, the Eukarya. Prokaryotes were the first inhabitants on Earth, perhaps appearing approximately 3.9 billion years ago. Today they are ubiquitous—inhabiting the harshest environments on the planet, from boiling hot springs to permanently frozen environments in Antarctica, as well as more benign environments such as compost heaps, soils, ocean waters, and the guts of animals (including humans). The Eukarya include the familiar kingdoms of animals, plants, and fungi. They also include a diverse group of kingdoms formerly grouped together as protists.

13.1 | Prokaryotic Diversity

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

- Describe the evolutionary history of prokaryotes
- Describe the basic structure of a typical prokaryote
- Identify bacterial diseases that caused historically important plagues and epidemics
- Describe the uses of prokaryotes in food processing and bioremediation

Prokaryotes are present everywhere. They cover every imaginable surface where there is sufficient moisture, and they live on and inside of other living things. There are more prokaryotes inside and on the exterior of the human body than there are human cells in the body. Some prokaryotes thrive in environments that are inhospitable for most other living things. Prokaryotes recycle nutrients—essential substances (such as carbon and nitrogen)—and they drive the evolution of new ecosystems, some of which are natural while others are man-made. Prokaryotes have been on Earth since long before multicellular life appeared.

Prokaryotic Diversity

The advent of DNA sequencing provided immense insight into the relationships and origins of prokaryotes that were not possible using traditional methods of classification. A major insight identified two groups of prokaryotes that were found to be as different from each other as they were from eukaryotes. This recognition of prokaryotic diversity forced a new understanding of the classification of all life and brought us closer to understanding the fundamental relationships of all living things, including ourselves.

Early Life on Earth

When and where did life begin? What were the conditions on Earth when life began? Prokaryotes were the first forms of life on Earth, and they existed for billions of years before plants and animals appeared. Earth is about 4.54 billion years old. This estimate is based on evidence from the dating of meteorite material, since surface rocks on Earth are not as old as Earth itself. Most rocks available on Earth have undergone geological changes that make them younger than Earth itself. Some meteorites are made of the original material in the solar disk that formed the objects of the solar system, and they have not been altered by the processes that altered rocks on Earth. Thus, the age of meteorites is a good indicator of the age of the formation of Earth. The original estimate of 4.54 billion years was obtained by Clare Patterson in 1956. His meticulous work has since been corroborated by ages determined from other sources, all of which point to an Earth age of about 4.54 billion years.

Early Earth had a very different atmosphere than it does today. Evidence indicates that during the first 2 billion years of Earth's existence, the atmosphere was **anoxic**, meaning that there was no oxygen. Therefore, only those organisms that can grow without oxygen—**anaerobic** organisms—were able to live. Organisms that convert solar energy into chemical energy are called **phototrophs**. Phototrophic organisms that required an organic source of carbon appeared within one billion years of the formation of Earth. Then, **cyanobacteria**, also known as blue-green algae, evolved from these simple phototrophs one billion years later. Cyanobacteria are able to use carbon dioxide as a source of carbon. Cyanobacteria (**Figure 13.2**) began the oxygenation of the atmosphere. The increase in oxygen concentration allowed the evolution of other life forms.



Figure 13.2 This hot spring in Yellowstone National Park flows toward the foreground. Cyanobacteria in the spring are green, and as water flows down the heat gradient, the intensity of the color increases because cell density increases. The water is cooler at the edges of the stream than in the center, causing the edges to appear greener. (credit: Graciela Brelles-Mariño)

Before the atmosphere became oxygenated, the planet was subjected to strong radiation; thus, the first organisms would have flourished where they were more protected, such as in ocean depths or beneath the surface of Earth. At this time, too, strong volcanic activity was common on Earth, so it is likely that these first organisms—the first prokaryotes—were adapted to very high temperatures. These are not the typical temperate environments in which most life flourishes today; thus, we can conclude that the first organisms that appeared on Earth likely were able to withstand harsh conditions.

Microbial mats may represent the earliest forms of life on Earth, and there is fossil evidence of their presence, starting about 3.5 billion years ago. A **microbial mat** is a large biofilm, a multi-layered sheet of prokaryotes (**Figure 13.3a**), including mostly bacteria, but also archaea. Microbial mats are a few centimeters thick, and they typically grow on moist surfaces. Their various types of prokaryotes carry out different metabolic pathways, and for this reason, they reflect various colors. Prokaryotes in a microbial mat are held together by a gummy-like substance that they secrete.

The first microbial mats likely obtained their energy from hydrothermal vents. A **hydrothermal vent** is a fissure in Earth's surface that releases geothermally heated water. With the evolution of photosynthesis about 3 billion years ago, some prokaryotes in microbial mats came to use a more widely available energy source—sunlight—whereas others were still dependent on chemicals from hydrothermal vents for food.

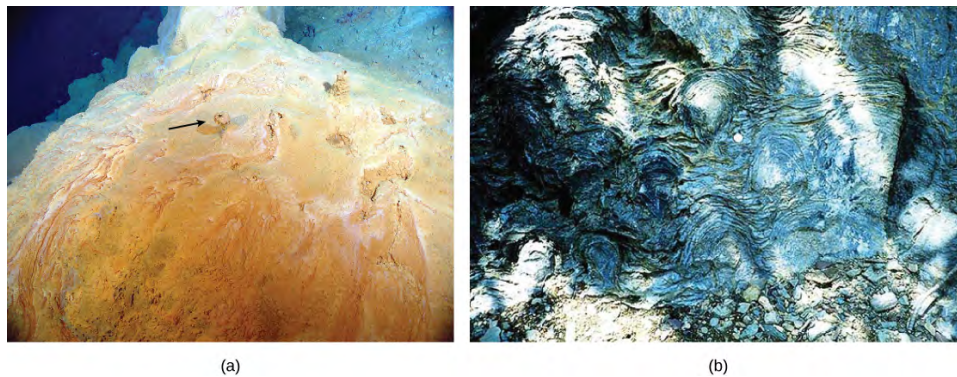


Figure 13.3 (a) This microbial mat grows over a hydrothermal vent in the Pacific Ocean. Chimneys such as the one indicated by the arrow allow gases to escape. (b) This photo shows stromatolites that are nearly 1.5 billion years old, found in Glacier National Park, Montana. (credit a: modification of work by Dr. Bob Embley, NOAA PMEL; credit b: modification of work by P. Carrara, NPS)

Fossilized microbial mats represent the earliest record of life on Earth. A **stromatolite** is a sedimentary structure formed when minerals are precipitated from water by prokaryotes in a microbial mat (**Figure 13.3b**). Stromatolites form layered rocks made of carbonate or silicate. Although most stromatolites are artifacts from the past, there are places on Earth where stromatolites are still forming. For example, living stromatolites have been found in the Anza-Borrego Desert State Park in San Diego County, California.

Some prokaryotes are able to thrive and grow under conditions that would kill a plant or animal. Bacteria and archaea that grow under extreme conditions are called **extremophiles**, meaning “lovers of extremes.” Extremophiles have been found in extreme environments of all kinds, including the depths of the oceans, hot springs, the Arctic and the Antarctic, very dry places, deep inside Earth, harsh chemical environments, and high radiation environments. Extremophiles give us a better understanding of prokaryotic diversity and open up the possibility of the discovery of new therapeutic drugs or industrial applications. They have also opened up the possibility of finding life in other places in the solar system, which have harsher environments than those typically found on Earth. Many of these extremophiles cannot survive in moderate environments.



Watch a **video** (<http://openstaxcollege.org/l/extremophiles>) showing the Director of the Planetary Science Division of NASA discussing the implications that the existence of extremophiles on Earth has on the possibility of finding life on other planets in our solar system, such as Mars.

Biofilms

Until a couple of decades ago, microbiologists thought of prokaryotes as isolated entities living apart. This model, however, does not reflect the true ecology of prokaryotes, most of which prefer to live in communities where they can interact. A **biofilm** is a microbial community held together in a gummy-textured matrix, consisting primarily of polysaccharides secreted by the organisms, together with some proteins and nucleic acids. Biofilms grow attached to surfaces. Some of the best-studied biofilms are composed of prokaryotes, although fungal biofilms have also been described.

Biofilms are present almost everywhere. They cause the clogging of pipes and readily colonize surfaces in industrial settings. They have played roles in recent, large-scale outbreaks of bacterial contamination of food. Biofilms also colonize household surfaces, such as kitchen counters, cutting boards, sinks, and toilets.

Interactions among the organisms that populate a biofilm, together with their protective environment, make these communities more robust than are free-living, or planktonic, prokaryotes. Overall, biofilms are very difficult to destroy, because they are resistant to many of the common forms of sterilization.

Characteristics of Prokaryotes

There are many differences between prokaryotic and eukaryotic cells. However, all cells have four common structures: a plasma membrane that functions as a barrier for the cell and separates the cell from its environment; cytoplasm, a jelly-like substance inside the cell; genetic material (DNA and RNA); and ribosomes, where protein synthesis takes place. Prokaryotes come in various shapes, but many fall into three categories: cocci (spherical), bacilli (rod-shaped), and spirilla (spiral-shaped) (**Figure 13.4**).

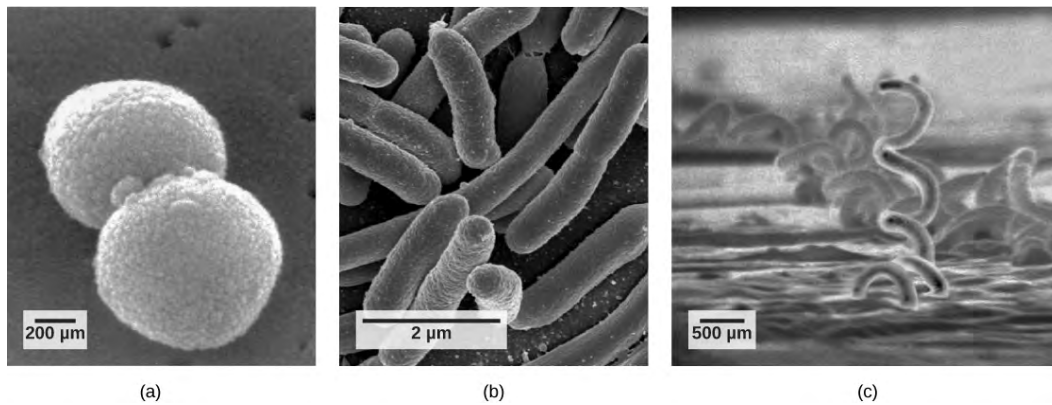


Figure 13.4 Many prokaryotes fall into three basic categories based on their shape: (a) cocci, or spherical; (b) bacilli, or rod-shaped; and (c) spirilla, or spiral-shaped. (credit a: modification of work by Janice Haney Carr, Dr. Richard Facklam, CDC; credit c: modification of work by Dr. David Cox, CDC; scale-bar data from Matt Russell)

The Prokaryotic Cell

Recall that prokaryotes (**Figure 13.5**) are unicellular organisms that lack organelles surrounded by membranes. Therefore, they do not have a nucleus but instead have a single chromosome—a piece of circular DNA located in an area of the cell called the nucleoid. Most prokaryotes have a cell wall lying outside the plasma membrane. The composition of the cell wall differs significantly between the domains Bacteria and Archaea (and their cell walls also differ from the eukaryotic cell walls found in plants and fungi.) The cell wall functions as a protective layer and is responsible for the organism's shape. Some other structures are present in some prokaryotic species, but not in others. For example, the **capsule** found in some species enables the organism to attach to surfaces and protects it from dehydration. Some species may also have flagella (singular, flagellum) used for locomotion, and pili (singular, pilus) used for attachment to surfaces and to other bacteria for conjugation. Plasmids, which consist of small, circular pieces of DNA outside of the main chromosome, are also present in many species of bacteria.

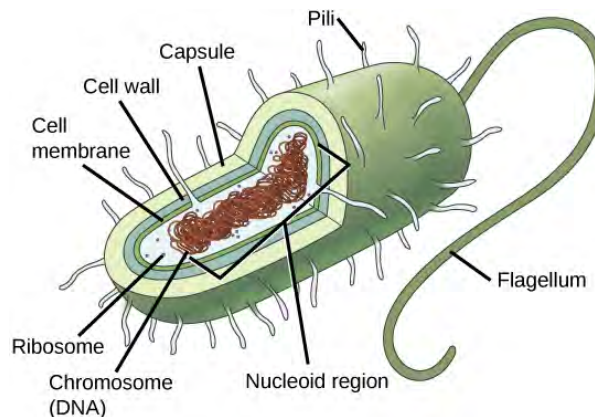


Figure 13.5 The features of a typical bacterium cell are shown.

Both Bacteria and Archaea are types of prokaryotic cells. They differ in the lipid composition of their cell membranes and in the characteristics of their cell walls. Both types of prokaryotes have the same basic structures, but these are built from different chemical components that are evidence of an ancient separation of their lineages. The archaeal plasma membrane is chemically different from the bacterial membrane; some archaeal membranes are lipid monolayers instead of phospholipid bilayers.

The Cell Wall

The cell wall is a protective layer that surrounds some prokaryotic cells and gives them shape and rigidity. It is located outside the cell membrane and prevents osmotic lysis (bursting caused by increasing volume). The chemical compositions of the cell walls vary between Archaea and Bacteria, as well as between bacterial species. Bacterial cell walls contain **peptidoglycan**, composed of polysaccharide chains cross-linked to peptides. Bacteria are divided into two major groups: **Gram-positive** and **Gram-negative**, based on their reaction to a procedure called Gram staining. The different bacterial responses to the staining procedure are caused by cell wall structure. Gram-positive organisms have a thick wall consisting

of many layers of peptidoglycan. Gram-negative bacteria have a thinner cell wall composed of a few layers of peptidoglycan and additional structures, surrounded by an outer membrane (Figure 13.6).

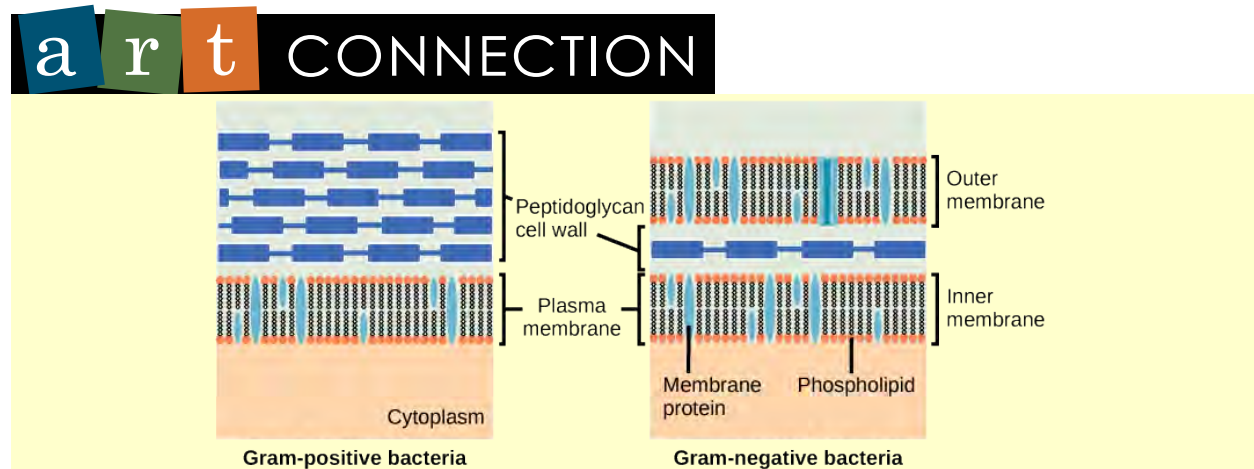


Figure 13.6 Bacteria are divided into two major groups: Gram-positive and Gram-negative. Both groups have a cell wall composed of peptidoglycans: In Gram-positive bacteria, the wall is thick, whereas in Gram-negative bacteria, the wall is thin. In Gram-negative bacteria, the cell wall is surrounded by an outer membrane.

Which of the following statements is true?

- Gram-positive bacteria have a single cell wall formed from peptidoglycan.
- Gram-positive bacteria have an outer membrane.
- The cell wall of Gram-negative bacteria is thick, and the cell wall of Gram-positive bacteria is thin.
- Gram-negative bacteria have a cell wall made of peptidoglycan, while Gram-positive bacteria have a cell wall made of phospholipids.

Archaeal cell walls do not contain peptidoglycan. There are four different types of archaeal cell walls. One type is composed of **pseudopeptidoglycan**. The other three types of cell walls contain polysaccharides, glycoproteins, and surface-layer proteins known as S-layers.

Reproduction

Reproduction in prokaryotes is primarily asexual and takes place by binary fission. Recall that the DNA of a prokaryote exists usually as a single, circular chromosome. Prokaryotes do not undergo mitosis. Rather, the chromosome loop is replicated, and the two resulting copies attached to the plasma membrane move apart as the cell grows in a process called binary fission. The prokaryote, now enlarged, is pinched inward at its equator, and the two resulting cells, which are clones, separate. Binary fission does not provide an opportunity for genetic recombination, but prokaryotes can alter their genetic makeup in three ways.

In a process called **transformation**, the cell takes in DNA found in its environment that is shed by other prokaryotes, alive or dead. A **pathogen** is an organism that causes a disease. If a nonpathogenic bacterium takes up DNA from a pathogen and incorporates the new DNA in its own chromosome, it too may become pathogenic. In **transduction**, bacteriophages, the viruses that infect bacteria, move DNA from one bacterium to another. Archaea have a different set of viruses that infect them and translocate genetic material from one individual to another. During **conjugation**, DNA is transferred from one prokaryote to another by means of a pilus that brings the organisms into contact with one another. The DNA transferred is usually a plasmid, but parts of the chromosome can also be moved.

Cycles of binary fission can be very rapid, on the order of minutes for some species. This short generation time coupled with mechanisms of genetic recombination result in the rapid evolution of prokaryotes, allowing them to respond to environmental changes (such as the introduction of an antibiotic) very quickly.

How Prokaryotes Obtain Energy and Carbon

Prokaryotes are metabolically diverse organisms. Prokaryotes fill many niches on Earth, including being involved in nutrient cycles such as the nitrogen and carbon cycles, decomposing dead organisms, and growing and multiplying inside living organisms, including humans. Different prokaryotes can use different sources of energy to assemble macromolecules

from smaller molecules. Phototrophs obtain their energy from sunlight. Chemotrophs obtain their energy from chemical compounds.

Bacterial Diseases in Humans

Devastating pathogen-borne diseases and plagues, both viral and bacterial in nature, have affected and continue to affect humans. It is worth noting that all pathogenic prokaryotes are Bacteria; there are no known pathogenic Archaea in humans or any other organism. Pathogenic organisms evolved alongside humans. In the past, the true cause of these diseases was not understood, and some cultures thought that diseases were a spiritual punishment or were mistaken about material causes. Over time, people came to realize that staying apart from afflicted persons, improving sanitation, and properly disposing of the corpses and personal belongings of victims of illness reduced their own chances of getting sick.

Historical Perspective

There are records of infectious diseases as far back as 3,000 B.C. A number of significant **pandemics** caused by Bacteria have been documented over several hundred years. Some of the largest pandemics led to the decline of cities and cultures. Many were zoonoses that appeared with the domestication of animals, as in the case of tuberculosis. A zoonosis is a disease that infects animals but can be transmitted from animals to humans.

Infectious diseases remain among the leading causes of death worldwide. Their impact is less significant in many developed countries, but they are important determiners of mortality in developing countries. The development of antibiotics did much to lessen the mortality rates from bacterial infections, but access to antibiotics is not universal, and the overuse of antibiotics has led to the development of resistant strains of bacteria. Public sanitation efforts that dispose of sewage and provide clean drinking water have done as much or more than medical advances to prevent deaths caused by bacterial infections.

In 430 B.C., the plague of Athens killed one-quarter of the Athenian troops that were fighting in the Great Peloponnesian War. The disease killed a quarter of the population of Athens in over 4 years and weakened Athens' dominance and power. The source of the plague may have been identified recently when researchers from the University of Athens were able to analyze DNA from teeth recovered from a mass grave. The scientists identified nucleotide sequences from a pathogenic bacterium that causes typhoid fever.^[1]

From 541 to 750 A.D., an outbreak called the plague of Justinian (likely a bubonic plague) eliminated, by some estimates, one-quarter to one-half of the human population. The population in Europe declined by 50 percent during this outbreak. Bubonic plague would decimate Europe more than once.

One of the most devastating pandemics was the **Black Death** (1346 to 1361), which is believed to have been another outbreak of bubonic plague caused by the bacterium *Yersinia pestis*. This bacterium is carried by fleas living on black rats. The Black Death reduced the world's population from an estimated 450 million to about 350 to 375 million. Bubonic plague struck London hard again in the mid-1600s. There are still approximately 1,000 to 3,000 cases of plague globally each year. Although contracting bubonic plague before antibiotics meant almost certain death, the bacterium responds to several types of modern antibiotics, and mortality rates from plague are now very low.



Watch a **video** (http://openstaxcollege.org/l/black_death2) on the modern understanding of the Black Death (bubonic plague) in Europe during the fourteenth century.

Over the centuries, Europeans developed resistance to many infectious diseases. However, European conquerors brought disease-causing bacteria and viruses with them when they reached the Western hemisphere, triggering **epidemics** that completely devastated populations of Native Americans (who had no natural resistance to many European diseases).

1. Papagrigorakis M. J., Synodinos P. N., Yapijakis C, "Ancient typhoid epidemic reveals possible ancestral strain of *Salmonella enterica* serovar Typhi, *Infect Genet Evol* 7 (2007): 126-7.

The Antibiotic Crisis

The word antibiotic comes from the Greek *anti*, meaning “against,” and *bios*, meaning “life.” An antibiotic is an organism-produced chemical that is hostile to the growth of other organisms. Today’s news and media often address concerns about an antibiotic crisis. Are antibiotics that were used to treat bacterial infections easily treatable in the past becoming obsolete? Are there new “superbugs”—bacteria that have evolved to become more resistant to our arsenal of antibiotics? Is this the beginning of the end of antibiotics? All of these questions challenge the healthcare community.

One of the main reasons for resistant bacteria is the overuse and incorrect use of antibiotics, such as not completing a full course of prescribed antibiotics. The incorrect use of an antibiotic results in the natural selection of resistant forms of bacteria. The antibiotic kills most of the infecting bacteria, and therefore only the resistant forms remain. These resistant forms reproduce, resulting in an increase in the proportion of resistant forms over non-resistant ones.

Another problem is the excessive use of antibiotics in livestock. The routine use of antibiotics in animal feed promotes bacterial resistance as well. In the United States, 70 percent of the antibiotics produced are fed to animals. The antibiotics are not used to prevent disease, but to enhance production of their products.



Watch a recent **news** (<http://openstaxcollege.org/l/antibiotics2>) report on the problem of routine antibiotic administration to livestock and antibiotic-resistant bacteria.

Staphylococcus aureus, often called “staph,” is a common bacterium that can live in and on the human body, which usually is easily treatable with antibiotics. A very dangerous strain, however, has made the news over the past few years (**Figure 13.7**). This strain, **methicillin-resistant *Staphylococcus aureus* (MRSA)**, is resistant to many commonly used antibiotics, including methicillin, amoxicillin, penicillin, and oxacillin. While MRSA infections have been common among people in healthcare facilities, it is appearing more commonly in healthy people who live or work in dense groups (like military personnel and prisoners). The *Journal of the American Medical Association* reported that, among MRSA-afflicted persons in healthcare facilities, the average age is 68 years, while people with “community-associated MRSA” (CA-MRSA) have an average age of 23 years.^[2]

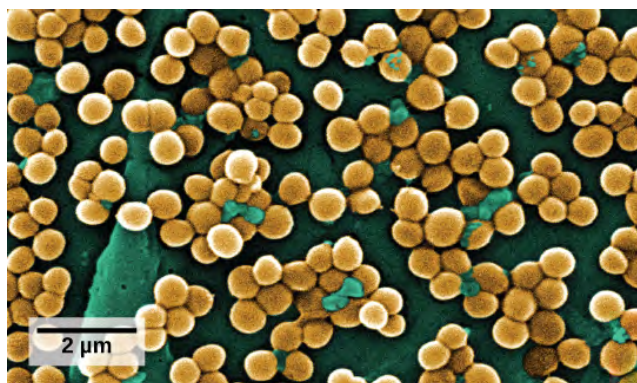


Figure 13.7 This scanning electron micrograph shows methicillin-resistant *Staphylococcus aureus* bacteria, commonly known as MRSA. (credit: modification of work by Janice Haney Carr, CDC; scale-bar data from Matt Russell)

In summary, society is facing an antibiotic crisis. Some scientists believe that after years of being protected from bacterial infections by antibiotics, we may be returning to a time in which a simple bacterial infection could again devastate the human population. Researchers are working on developing new antibiotics, but few are in the drug development pipeline, and it takes many years to generate an effective and approved drug.

2. Naimi, T. S., LeDell, K. H., Como-Sabetti, K., et al., “Comparison of community- and health care-associated methicillin-resistant *Staphylococcus aureus* infection,” *JAMA* 290 (2003): 2976-2984, doi: 10.1001/jama.290.22.2976.

Foodborne Diseases

Prokaryotes are everywhere: They readily colonize the surface of any type of material, and food is not an exception. Outbreaks of bacterial infection related to food consumption are common. A **foodborne disease** (colloquially called “food poisoning”) is an illness resulting from the consumption of food contaminated with pathogenic bacteria, viruses, or other parasites. Although the United States has one of the safest food supplies in the world, the Center for Disease Control and Prevention (CDC) has reported that “76 million people get sick, more than 300,000 are hospitalized, and 5,000 Americans die each year from foodborne illness.”^[3]

The characteristics of foodborne illnesses have changed over time. In the past, it was relatively common to hear about sporadic cases of **botulism**, the potentially fatal disease produced by a toxin from the anaerobic bacterium *Clostridium botulinum*. A can, jar, or package created a suitable anaerobic environment where *Clostridium* could grow. Proper sterilization and canning procedures have reduced the incidence of this disease.

Most cases of foodborne illnesses are now linked to produce contaminated by animal waste. For example, there have been serious, produce-related outbreaks associated with raw spinach in the United States and with vegetable sprouts in Germany (**Figure 13.8**). The raw spinach outbreak in 2006 was produced by the bacterium *E. coli* strain O157:H7. Most *E. coli* strains are not particularly dangerous to humans, (indeed, they live in our large intestine), but O157:H7 is potentially fatal.

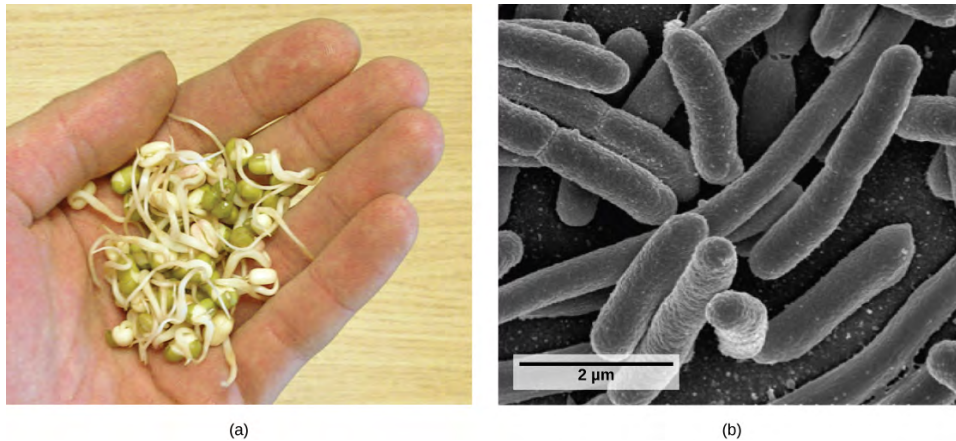


Figure 13.8 (a) Locally grown vegetable sprouts were the cause of a European *E. coli* outbreak that killed 31 people and sickened about 3,000 in 2010. (b) *Escherichia coli* are shown here in a scanning electron micrograph. The strain of *E. coli* that caused a deadly outbreak in Germany is a new one not involved in any previous *E. coli* outbreaks. It has acquired several antibiotic resistance genes and specific genetic sequences involved in aggregation ability and virulence. It has recently been sequenced. (credit b: Rocky Mountain Laboratories, NIAID, NIH; scale-bar data from Matt Russell)

All types of food can potentially be contaminated with harmful bacteria of different species. Recent outbreaks of *Salmonella* reported by the CDC occurred in foods as diverse as peanut butter, alfalfa sprouts, and eggs.

3. <http://www.cdc.gov/ecoli/2006/september>, Centers for Disease Control and Prevention, “Multi-state outbreak of *E. coli* O157:H7 infections from spinach,” September-October (2006).

careers IN ACTION

Epidemiologist

Epidemiology is the study of the occurrence, distribution, and determinants of health and disease in a population. It is, therefore, related to public health. An epidemiologist studies the frequency and distribution of diseases within human populations and environments.

Epidemiologists collect data about a particular disease and track its spread to identify the original mode of transmission. They sometimes work in close collaboration with historians to try to understand the way a disease evolved geographically and over time, tracking the natural history of pathogens. They gather information from clinical records, patient interviews, and any other available means. That information is used to develop strategies and design public health policies to reduce the incidence of a disease or to prevent its spread. Epidemiologists also conduct rapid investigations in case of an outbreak to recommend immediate measures to control it.

Epidemiologists typically have a graduate-level education. An epidemiologist often has a bachelor's degree in some field and a master's degree in public health (MPH). Many epidemiologists are also physicians (and have an MD) or they have a PhD in an associated field, such as biology or epidemiology.

Beneficial Prokaryotes

Not all prokaryotes are pathogenic. On the contrary, pathogens represent only a very small percentage of the diversity of the microbial world. In fact, our life and all life on this planet would not be possible without prokaryotes.

Prokaryotes, and Food and Beverages

According to the United Nations Convention on Biological Diversity, biotechnology is “any technological application that uses biological systems, living organisms, or derivatives thereof, to make or modify products or processes for specific use.”^[4] The concept of “specific use” involves some sort of commercial application. Genetic engineering, artificial selection, antibiotic production, and cell culture are current topics of study in biotechnology. However, humans have used prokaryotes to create products before the term biotechnology was even coined. And some of the goods and services are as simple as cheese, yogurt, sour cream, vinegar, cured sausage, sauerkraut, and fermented seafood that contains both bacteria and archaea (**Figure 13.9**).

4. <http://www.cbd.int/convention/articles/?a=cbd-02><http://www.cbd.int/convention/articles/?a=cbd-02>, United Nations Convention on Biological Diversity, “Article 2: Use of Terms.”

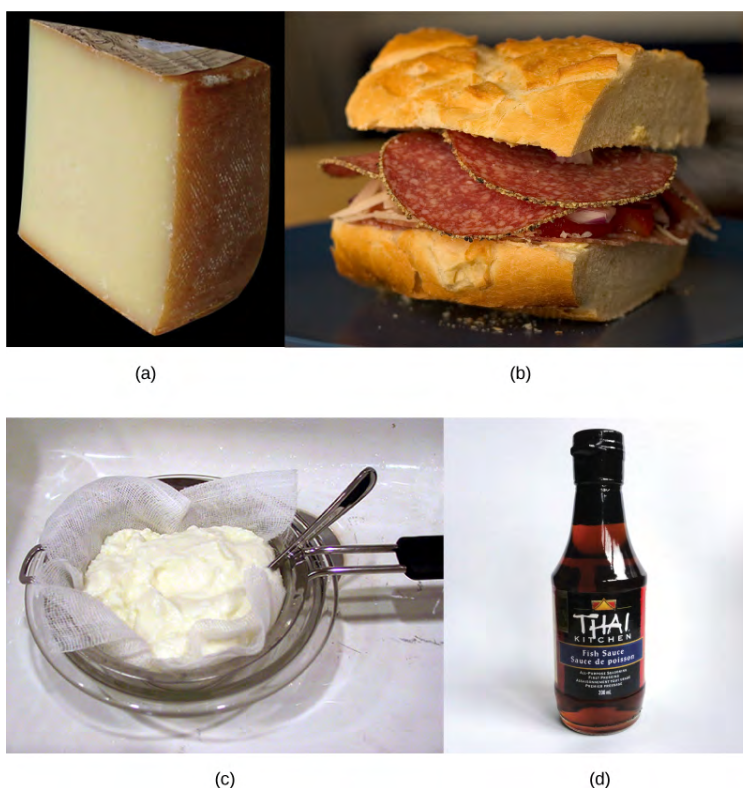


Figure 13.9 Some of the products derived from the use of prokaryotes in early biotechnology include (a) cheese, (b) salami, (c) yogurt, and (d) fish sauce. (credit b: modification of work by Alisdair McDiarmid; credit c: modification of work by Kris Miller; credit d: modification of work by Jane Whitney)

Cheese production began around 4,000 years ago when humans started to breed animals and process their milk. Evidence suggests that cultured milk products, like yogurt, have existed for at least 4,000 years.

Using Prokaryotes to Clean up Our Planet: Bioremediation

Microbial **bioremediation** is the use of prokaryotes (or microbial metabolism) to remove pollutants. Bioremediation has been used to remove agricultural chemicals (pesticides and fertilizers) that leach from soil into groundwater. Certain toxic metals, such as selenium and arsenic compounds, can also be removed from water by bioremediation. The reduction of SeO_4^{2-} to SeO_3^{2-} and to Se^0 (metallic selenium) is a method used to remove selenium ions from water. Mercury is an example of a toxic metal that can be removed from an environment by bioremediation. Mercury is an active ingredient of some pesticides; it is used in industry and is also a byproduct of certain industries, such as battery production. Mercury is usually present in very low concentrations in natural environments but it is highly toxic because it accumulates in living tissues. Several species of bacteria can carry out the biotransformation of toxic mercury into nontoxic forms. These bacteria, such as *Pseudomonas aeruginosa*, can convert Hg^{2+} to Hg^0 , which is nontoxic to humans.

Probably one of the most useful and interesting examples of the use of prokaryotes for bioremediation purposes is the cleanup of oil spills. The importance of prokaryotes to petroleum bioremediation has been demonstrated in several oil spills in recent years, such as the Exxon Valdez spill in Alaska (1989) (**Figure 13.10**), the Prestige oil spill in Spain (2002), the spill into the Mediterranean from a Lebanon power plant (2006,) and more recently, the BP oil spill in the Gulf of Mexico (2010). To clean up these spills, bioremediation is promoted by adding inorganic nutrients that help bacteria already present in the environment to grow. Hydrocarbon-degrading bacteria feed on the hydrocarbons in the oil droplet, breaking them into inorganic compounds. Some species, such as *Alcanivorax borkumensis*, produce surfactants that solubilize the oil, while other bacteria degrade the oil into carbon dioxide. In the case of oil spills in the ocean, ongoing, natural bioremediation tends to occur, inasmuch as there are oil-consuming bacteria in the ocean prior to the spill. Under ideal conditions, it has been reported that up to 80 percent of the nonvolatile components in oil can be degraded within 1 year of the spill. Other oil fractions containing aromatic and highly branched hydrocarbon chains are more difficult to remove and remain in the environment for longer periods of time. Researchers have genetically engineered other bacteria to consume petroleum products; indeed, the first patent application for a bioremediation application in the U.S. was for a genetically modified oil-eating bacterium.



Figure 13.10 (a) Cleaning up oil after the Valdez spill in Alaska, the workers hosed oil from beaches and then used a floating boom to corral the oil, which was finally skimmed from the water surface. Some species of bacteria are able to solubilize and degrade the oil. (b) One of the most catastrophic consequences of oil spills is the damage to fauna. (credit a: modification of work by NOAA; credit b: modification of work by GOLUBENKOV, NGO: Saving Taman)

Prokaryotes in and on the Body

Humans are no exception when it comes to forming symbiotic relationships with prokaryotes. We are accustomed to thinking of ourselves as single organisms, but in reality, we are walking ecosystems. There are 10 to 100 times as many bacterial and archaeal cells inhabiting our bodies as we have cells in our bodies. Some of these are in mutually beneficial relationships with us, in which both the human host and the bacterium benefit, while some of the relationships are classified as **commensalism**, a type of relationship in which the bacterium benefits and the human host is neither benefited nor harmed.

Human gut flora lives in the large intestine and consists of hundreds of species of bacteria and archaea, with different individuals containing different species mixes. The term “flora,” which is usually associated with plants, is traditionally used in this context because bacteria were once classified as plants. The primary functions of these prokaryotes for humans appear to be metabolism of food molecules that we cannot break down, assistance with the absorption of ions by the colon, synthesis of vitamin K, training of the infant immune system, maintenance of the adult immune system, maintenance of the epithelium of the large intestine, and formation of a protective barrier against pathogens.

The surface of the skin is also coated with prokaryotes. The different surfaces of the skin, such as the underarms, the head, and the hands, provide different habitats for different communities of prokaryotes. Unlike with gut flora, the possible beneficial roles of skin flora have not been well studied. However, the few studies conducted so far have identified bacteria that produce antimicrobial compounds as probably responsible for preventing infections by pathogenic bacteria.

Researchers are actively studying the relationships between various diseases and alterations to the composition of human microbial flora. Some of this work is being carried out by the Human Microbiome Project, funded in the United States by the National Institutes of Health.

13.2 | Eukaryotic Origins

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

- Describe the endosymbiotic theory
- Explain the origin of mitochondria and chloroplasts

The fossil record and genetic evidence suggest that prokaryotic cells were the first organisms on Earth. These cells originated approximately 3.5 billion years ago, which was about 1 billion years after Earth’s formation, and were the only life forms on the planet until eukaryotic cells emerged approximately 2.1 billion years ago. During the prokaryotic reign, photosynthetic prokaryotes evolved that were capable of applying the energy from sunlight to synthesize organic materials (like carbohydrates) from carbon dioxide and an electron source (such as hydrogen, hydrogen sulfide, or water).

Photosynthesis using water as an electron donor consumes carbon dioxide and releases molecular oxygen (O_2) as a byproduct. The functioning of photosynthetic bacteria over millions of years progressively saturated Earth’s water with oxygen and then oxygenated the atmosphere, which previously contained much greater concentrations of carbon dioxide and much lower concentrations of oxygen. Older anaerobic prokaryotes of the era could not function in their new, aerobic environment. Some species perished, while others survived in the remaining anaerobic environments left on Earth. Still other early prokaryotes evolved mechanisms, such as aerobic respiration, to exploit the oxygenated atmosphere by using

oxygen to store energy contained within organic molecules. Aerobic respiration is a more efficient way of obtaining energy from organic molecules, which contributed to the success of these species (as evidenced by the number and diversity of aerobic organisms living on Earth today). The evolution of aerobic prokaryotes was an important step toward the evolution of the first eukaryote, but several other distinguishing features had to evolve as well.

Endosymbiosis

The origin of eukaryotic cells was largely a mystery until a revolutionary hypothesis was comprehensively examined in the 1960s by Lynn Margulis. The **endosymbiotic theory** states that eukaryotes are a product of one prokaryotic cell engulfing another, one living within another, and evolving together over time until the separate cells were no longer recognizable as such. This once-revolutionary hypothesis had immediate persuasiveness and is now widely accepted, with work progressing on uncovering the steps involved in this evolutionary process as well as the key players. It has become clear that many nuclear eukaryotic genes and the molecular machinery responsible for replicating and expressing those genes appear closely related to the Archaea. On the other hand, the metabolic organelles and the genes responsible for many energy-harvesting processes had their origins in bacteria. Much remains to be clarified about how this relationship occurred; this continues to be an exciting field of discovery in biology. Several endosymbiotic events likely contributed to the origin of the eukaryotic cell.

Mitochondria

Eukaryotic cells may contain anywhere from one to several thousand mitochondria, depending on the cell's level of energy consumption. Each mitochondrion measures 1 to 10 micrometers in length and exists in the cell as a moving, fusing, and dividing oblong spheroid (**Figure 13.11**). However, mitochondria cannot survive outside the cell. As the atmosphere was oxygenated by photosynthesis, and as successful aerobic prokaryotes evolved, evidence suggests that an ancestral cell engulfed and kept alive a free-living, aerobic prokaryote. This gave the host cell the ability to use oxygen to release energy stored in nutrients. Several lines of evidence support that mitochondria are derived from this endosymbiotic event. Mitochondria are shaped like a specific group of bacteria and are surrounded by two membranes, which would result when one membrane-bound organism was engulfed by another membrane-bound organism. The mitochondrial inner membrane involves substantial infoldings or cristae that resemble the textured outer surface of certain bacteria.

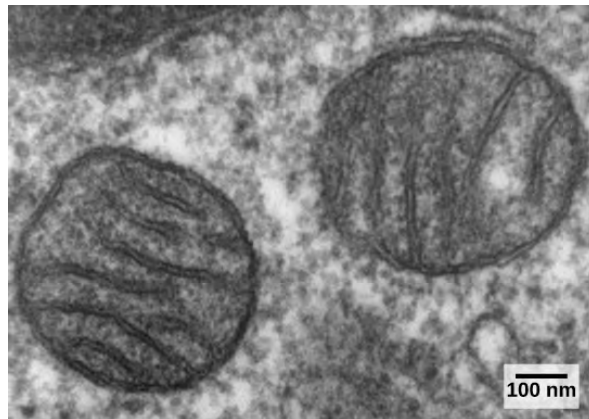


Figure 13.11 In this transmission electron micrograph of mitochondria in a mammalian lung cell, the cristae, infoldings of the mitochondrial inner membrane, can be seen in cross-section. (credit: modification of work by Louisa Howard; scale-bar data from Matt Russell)

Mitochondria divide on their own by a process that resembles binary fission in prokaryotes. Mitochondria have their own circular DNA chromosome that carries genes similar to those expressed by bacteria. Mitochondria also have special ribosomes and transfer RNAs that resemble these components in prokaryotes. These features all support that mitochondria were once free-living prokaryotes.

Chloroplasts

Chloroplasts are one type of **plastid**, a group of related organelles in plant cells that are involved in the storage of starches, fats, proteins, and pigments. Chloroplasts contain the green pigment chlorophyll and play a role in photosynthesis. Genetic and morphological studies suggest that plastids evolved from the endosymbiosis of an ancestral cell that engulfed a photosynthetic cyanobacterium. Plastids are similar in size and shape to cyanobacteria and are enveloped by two or more membranes, corresponding to the inner and outer membranes of cyanobacteria. Like mitochondria, plastids also contain circular genomes and divide by a process reminiscent of prokaryotic cell division. The chloroplasts of red and green algae

exhibit DNA sequences that are closely related to photosynthetic cyanobacteria, suggesting that red and green algae are direct descendants of this endosymbiotic event.

Mitochondria likely evolved before plastids because all eukaryotes have either functional mitochondria or mitochondria-like organelles. In contrast, plastids are only found in a subset of eukaryotes, such as terrestrial plants and algae. One hypothesis of the evolutionary steps leading to the first eukaryote is summarized in **Figure 13.12**.

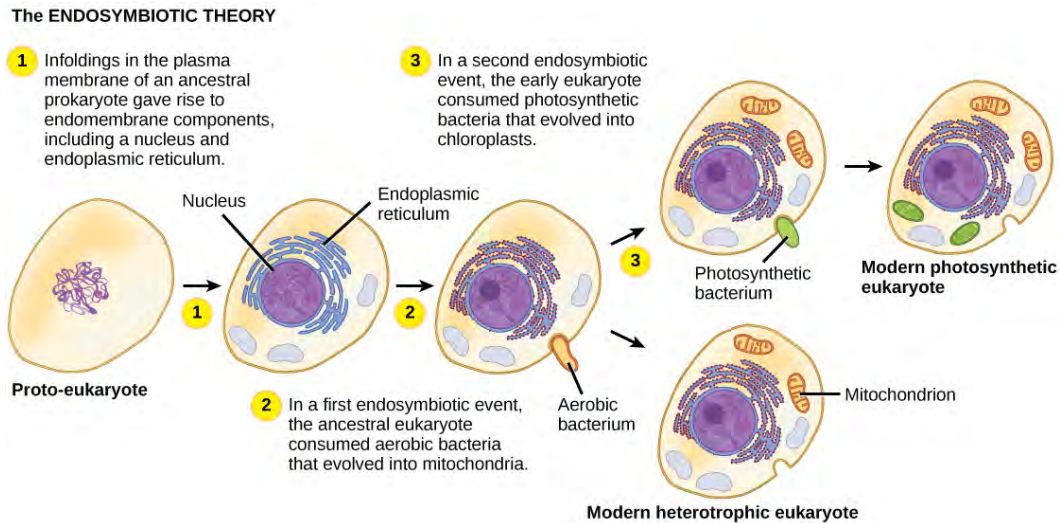


Figure 13.12 The first eukaryote may have originated from an ancestral prokaryote that had undergone membrane proliferation, compartmentalization of cellular function (into a nucleus, lysosomes, and an endoplasmic reticulum), and the establishment of endosymbiotic relationships with an aerobic prokaryote and, in some cases, a photosynthetic prokaryote to form mitochondria and chloroplasts, respectively.

The exact steps leading to the first eukaryotic cell can only be hypothesized, and some controversy exists regarding which events actually took place and in what order. Spirochete bacteria have been hypothesized to have given rise to microtubules, and a flagellated prokaryote may have contributed the raw materials for eukaryotic flagella and cilia. Other scientists suggest that membrane proliferation and compartmentalization, not endosymbiotic events, led to the development of mitochondria and plastids. However, the vast majority of studies support the endosymbiotic hypothesis of eukaryotic evolution.

The early eukaryotes were unicellular like most protists are today, but as eukaryotes became more complex, the evolution of multicellularity allowed cells to remain small while still exhibiting specialized functions. The ancestors of today's multicellular eukaryotes are thought to have evolved about 1.5 billion years ago.

13.3 | Protists

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

- Describe the main characteristics of protists
- Describe important pathogenic species of protists
- Describe the roles of protists as food sources and as decomposers

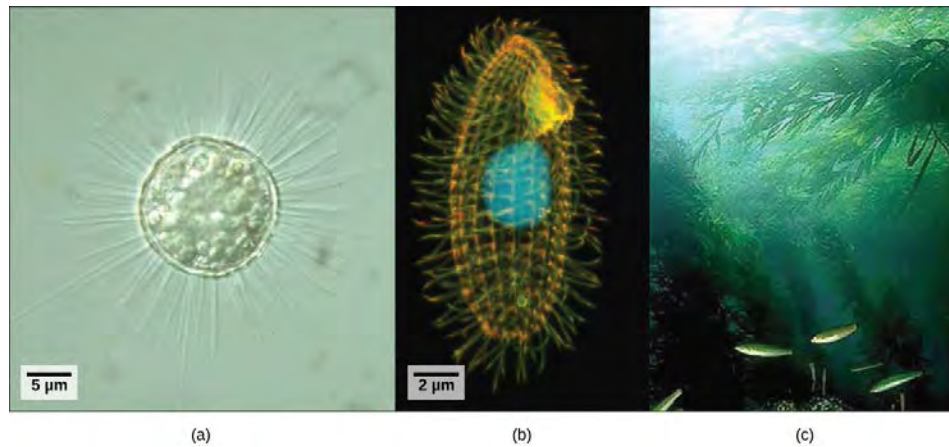


Figure 13.13 Protists range from the microscopic, single-celled (a) *Acanthocystis turfacea* and the (b) ciliate *Tetrahymena thermophila* to the enormous, multicellular (c) kelps (Chromalveolata) that extend for hundreds of feet in underwater “forests.” (credit a: modification of work by Yuiuji Tsukii; credit b: modification of work by Richard Robinson, Public Library of Science; credit c: modification of work by Kip Evans, NOAA; scale-bar data from Matt Russell)

Eukaryotic organisms that did not fit the criteria for the kingdoms Animalia, Fungi, or Plantae historically were called protists and were classified into the kingdom Protista. Protists include the single-celled eukaryotes living in pond water (Figure 13.13), although protist species live in a variety of other aquatic and terrestrial environments, and occupy many different niches. Not all protists are microscopic and single-celled; there exist some very large multicellular species, such as the kelps. During the past two decades, the field of molecular genetics has demonstrated that some protists are more related to animals, plants, or fungi than they are to other protists. For this reason, protist lineages originally classified into the kingdom Protista have been reassigned into new kingdoms or other existing kingdoms. The evolutionary lineages of the protists continue to be examined and debated. In the meantime, the term “protist” still is used informally to describe this tremendously diverse group of eukaryotes. As a collective group, protists display an astounding diversity of morphologies, physiologies, and ecologies.

Characteristics of Protists

There are over 100,000 described living species of protists, and it is unclear how many undescribed species may exist. Since many protists live in symbiotic relationships with other organisms and these relationships are often species specific, there is a huge potential for undescribed protist diversity that matches the diversity of the hosts. As the catchall term for eukaryotic organisms that are not animals, plants, fungi, or any single phylogenetically related group, it is not surprising that few characteristics are common to all protists.

Nearly all protists exist in some type of aquatic environment, including freshwater and marine environments, damp soil, and even snow. Several protist species are **parasites** that infect animals or plants. A parasite is an organism that lives on or in another organism and feeds on it, often without killing it. A few protist species live on dead organisms or their wastes, and contribute to their decay.

Protist Structure

The cells of protists are among the most elaborate of all cells. Most protists are microscopic and unicellular, but some true multicellular forms exist. A few protists live as colonies that behave in some ways as a group of free-living cells and in other ways as a multicellular organism. Still other protists are composed of enormous, multinucleate, single cells that look like amorphous blobs of slime or, in other cases, like ferns. In fact, many protist cells are multinucleated; in some species, the nuclei are different sizes and have distinct roles in protist cell function.

Single protist cells range in size from less than a micrometer to the 3-meter lengths of the multinucleate cells of the seaweed *Caulerpa*. Protist cells may be enveloped by animal-like cell membranes or plant-like cell walls. Others are encased in glassy silica-based shells or wound with **pellicles** of interlocking protein strips. The pellicle functions like a flexible coat of armor, preventing the protist from being torn or pierced without compromising its range of motion.

The majority of protists are motile, but different types of protists have evolved varied modes of movement. Some protists have one or more flagella, which they rotate or whip. Others are covered in rows or tufts of tiny cilia that they beat in coordination to swim. Still others send out lobe-like pseudopodia from anywhere on the cell, anchor the pseudopodium to a substrate, and pull the rest of the cell toward the anchor point. Some protists can move toward light by coupling their locomotion strategy with a light-sensing organ.

How Protists Obtain Energy

Protists exhibit many forms of nutrition and may be aerobic or anaerobic. Photosynthetic protists (photoautotrophs) are characterized by the presence of chloroplasts. Other protists are heterotrophs and consume organic materials (such as other organisms) to obtain nutrition. Amoebas and some other heterotrophic protist species ingest particles by a process called phagocytosis, in which the cell membrane engulfs a food particle and brings it inward, pinching off an intracellular membranous sac, or vesicle, called a food vacuole (Figure 13.14). This vesicle then fuses with a lysosome, and the food particle is broken down into small molecules that can diffuse into the cytoplasm and be used in cellular metabolism. Undigested remains ultimately are expelled from the cell through exocytosis.

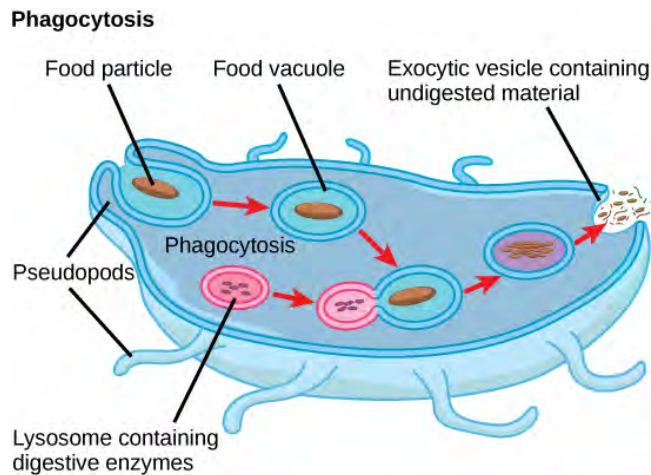


Figure 13.14 The stages of phagocytosis include the engulfment of a food particle, the digestion of the particle using hydrolytic enzymes contained within a lysosome, and the expulsion of undigested material from the cell.

Some heterotrophs absorb nutrients from dead organisms or their organic wastes, and others are able to use photosynthesis or feed on organic matter, depending on conditions.

Reproduction

Protists reproduce by a variety of mechanisms. Most are capable some form of asexual reproduction, such as binary fission to produce two daughter cells, or multiple fission to divide simultaneously into many daughter cells. Others produce tiny buds that go on to divide and grow to the size of the parental protist. Sexual reproduction, involving meiosis and fertilization, is common among protists, and many protist species can switch from asexual to sexual reproduction when necessary. Sexual reproduction is often associated with periods when nutrients are depleted or environmental changes occur. Sexual reproduction may allow the protist to recombine genes and produce new variations of progeny that may be better suited to surviving in the new environment. However, sexual reproduction is also often associated with cysts that are a protective, resting stage. Depending on their habitat, the cysts may be particularly resistant to temperature extremes, desiccation, or low pH. This strategy also allows certain protists to “wait out” stressors until their environment becomes more favorable for survival or until they are carried (such as by wind, water, or transport on a larger organism) to a different environment because cysts exhibit virtually no cellular metabolism.

Protist Diversity

With the advent of DNA sequencing, the relationships among protist groups and between protist groups and other eukaryotes are beginning to become clearer. Many relationships that were based on morphological similarities are being replaced by new relationships based on genetic similarities. Protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon is called convergent evolution. It is one reason why protist classification is so challenging. The emerging classification scheme groups the entire domain Eukaryota into six “supergroups” that contain all of the protists as well as animals, plants, and fungi (Figure 13.15); these include the **Excavata**, **Chromalveolata**, **Rhizaria**, **Archaeplastida**, **Amoebozoa**, and **Opisthokonta**. The supergroups are believed to be monophyletic; all organisms within each supergroup are believed to have evolved from a single common ancestor, and thus all members are most closely related to each other than to organisms outside that group. There is still evidence lacking for the monophyly of some groups.

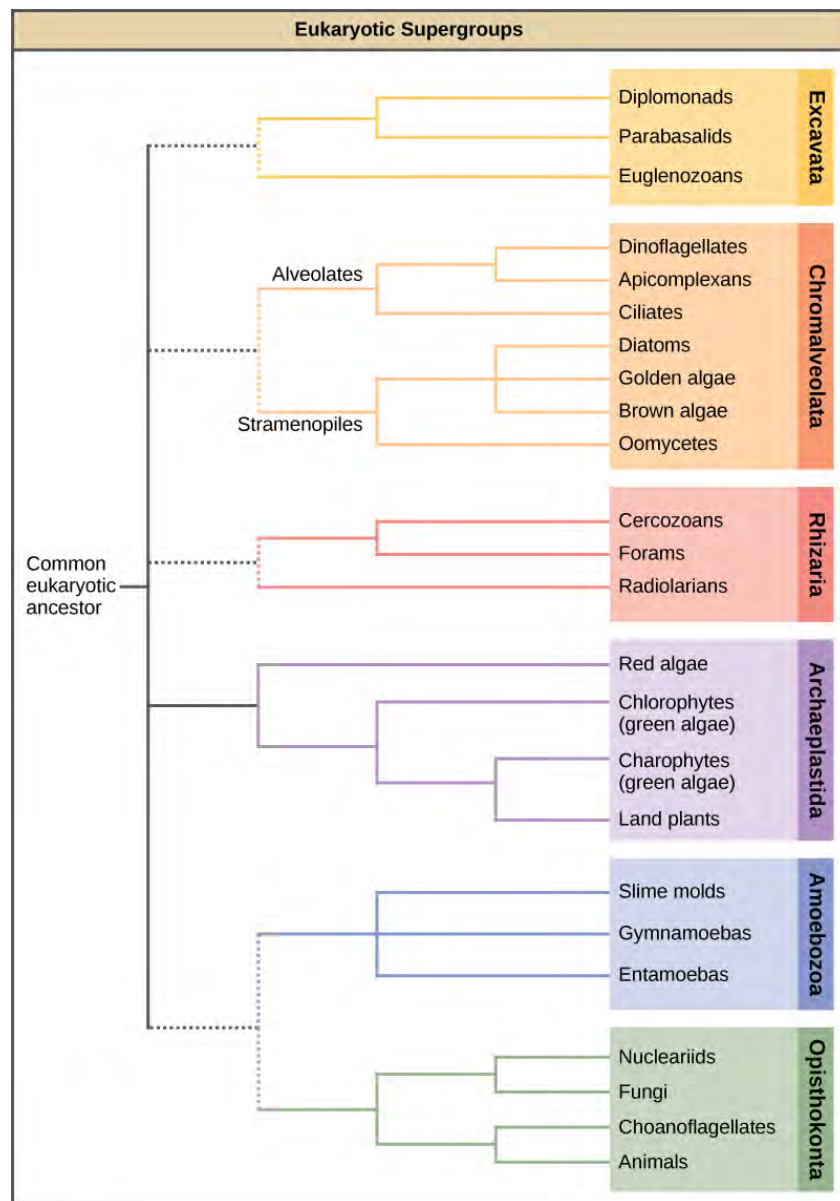


Figure 13.15 Protists appear in all six eukaryotic supergroups.

Human Pathogens

Many protists are pathogenic parasites that must infect other organisms to survive and propagate. Protist parasites include the causative agents of malaria, African sleeping sickness, and waterborne gastroenteritis in humans. Other protist pathogens prey on plants, effecting massive destruction of food crops.

Plasmodium Species

Members of the genus *Plasmodium* must infect a mosquito and a vertebrate to complete their life cycle. In vertebrates, the parasite develops in liver cells and goes on to infect red blood cells, bursting from and destroying the blood cells with each asexual replication cycle (Figure 13.16). Of the four *Plasmodium* species known to infect humans, *P. falciparum* accounts for 50 percent of all malaria cases and is the primary cause of disease-related fatalities in tropical regions of the world. In 2010, it was estimated that malaria caused between 0.5 and 1 million deaths, mostly in African children. During the course of malaria, *P. falciparum* can infect and destroy more than one-half of a human's circulating blood cells, leading to severe anemia. In response to waste products released as the parasites burst from infected blood cells, the host immune system mounts a massive inflammatory response with delirium-inducing fever episodes, as parasites destroy red blood cells, spilling parasite waste into the blood stream. *P. falciparum* is transmitted to humans by the African malaria mosquito, *Anopheles gambiae*. Techniques to kill, sterilize, or avoid exposure to this highly aggressive mosquito species are crucial to malaria control.

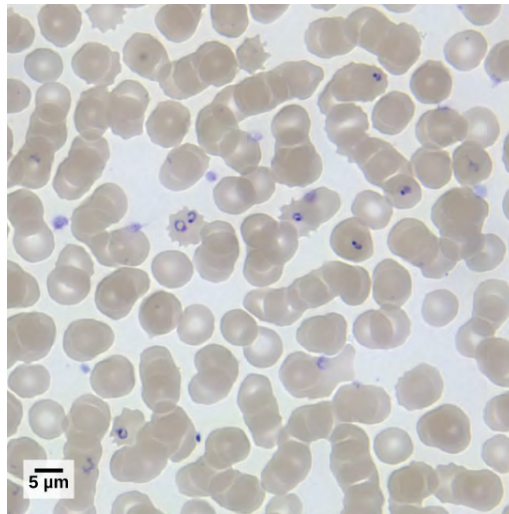


Figure 13.16 This light micrograph shows a 100× magnification of red blood cells infected with *P. falciparum* (seen as purple). (credit: modification of work by Michael Zahniser; scale-bar data from Matt Russell)



This **movie** (<http://openstaxcollege.org/l/malaria2>) depicts the pathogenesis of *Plasmodium falciparum*, the causative agent of malaria.

Trypanosomes

T. brucei, the parasite that is responsible for African sleeping sickness, confounds the human immune system by changing its thick layer of surface glycoproteins with each infectious cycle (**Figure 13.17**). The glycoproteins are identified by the immune system as foreign matter, and a specific antibody defense is mounted against the parasite. However, *T. brucei* has thousands of possible antigens, and with each subsequent generation, the protist switches to a glycoprotein coating with a different molecular structure. In this way, *T. brucei* is capable of replicating continuously without the immune system ever succeeding in clearing the parasite. Without treatment, African sleeping sickness leads invariably to death because of damage it does to the nervous system. During epidemic periods, mortality from the disease can be high. Greater surveillance and control measures have led to a reduction in reported cases; some of the lowest numbers reported in 50 years (fewer than 10,000 cases in all of sub-Saharan Africa) have happened since 2009.

In Latin America, another species in the genus, *T. cruzi*, is responsible for Chagas disease. *T. cruzi* infections are mainly caused by a blood-sucking bug. The parasite inhabits heart and digestive system tissues in the chronic phase of infection, leading to malnutrition and heart failure caused by abnormal heart rhythms. An estimated 10 million people are infected with Chagas disease, which caused 10,000 deaths in 2008.

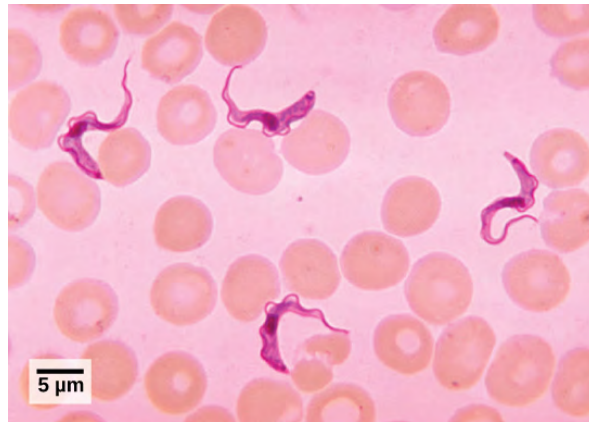


Figure 13.17 Trypanosomes are shown in this light micrograph among red blood cells. (credit: modification of work by Myron G. Schultz, CDC; scale-bar data from Matt Russell)

CONCEPT in ACTION



This **movie** (http://openstaxcollege.org/l/African_sleep2) discusses the pathogenesis of *Trypanosoma brucei*, the causative agent of African sleeping sickness.

Plant Parasites

Protist parasites of terrestrial plants include agents that destroy food crops. The oomycete *Plasmopara viticola* parasitizes grape plants, causing a disease called downy mildew (**Figure 13.18a**). Grape plants infected with *P. viticola* appear stunted and have discolored withered leaves. The spread of downy mildew caused the near collapse of the French wine industry in the nineteenth century.



Figure 13.18 (a) The downy and powdery mildews on this grape leaf are caused by an infection of *P. viticola*. (b) This potato exhibits the results of an infection with *P. infestans*, the potato late blight. (credit a: modification of work by David B. Langston, University of Georgia, USDA ARS; credit b: USDA ARS)

Phytophthora infestans is an oomycete responsible for potato late blight, which causes potato stalks and stems to decay into black slime (**Figure 13.18b**). Widespread potato blight caused by *P. infestans* precipitated the well-known Irish potato famine in the nineteenth century that claimed the lives of approximately 1 million people and led to the emigration from Ireland of at least 1 million more. Late blight continues to plague potato crops in certain parts of the United States and Russia, wiping out as much as 70 percent of crops when no pesticides are applied.

Beneficial Protists

Protists play critically important ecological roles as producers particularly in the world's oceans. They are equally important on the other end of food webs as decomposers.

Protists as Food Sources

Protists are essential sources of nutrition for many other organisms. In some cases, as in plankton, protists are consumed directly. Alternatively, photosynthetic protists serve as producers of nutrition for other organisms by carbon fixation. For instance, photosynthetic dinoflagellates called zooxanthellae pass on most of their energy to the coral polyps that house them (**Figure 13.19**). In this mutually beneficial relationship, the polyps provide a protective environment and nutrients for the zooxanthellae. The polyps secrete the calcium carbonate that builds coral reefs. Without dinoflagellate symbionts, corals lose algal pigments in a process called coral bleaching, and they eventually die. This explains why reef-building corals do not reside in waters deeper than 20 meters: Not enough light reaches those depths for dinoflagellates to photosynthesize.



Figure 13.19 Coral polyps obtain nutrition through a symbiotic relationship with dinoflagellates.

Protists themselves and their products of photosynthesis are essential—directly or indirectly—to the survival of organisms ranging from bacteria to mammals. As primary producers, protists feed a large proportion of the world's aquatic species. (On land, terrestrial plants serve as primary producers.) In fact, approximately one-quarter of the world's photosynthesis is conducted by protists, particularly dinoflagellates, diatoms, and multicellular algae.

Protists do not create food sources only for sea-dwelling organisms. For instance, certain anaerobic species exist in the digestive tracts of termites and wood-eating cockroaches, where they contribute to digesting cellulose ingested by these insects as they bore through wood. The actual enzyme used to digest the cellulose is actually produced by bacteria living within the protist cells. The termite provides the food source to the protist and its bacteria, and the protist and bacteria provide nutrients to the termite by breaking down the cellulose.

Agents of Decomposition

Many fungus-like protists are **saprobies**, organisms that feed on dead organisms or the waste matter produced by organisms (saprophyte is an equivalent term), and are specialized to absorb nutrients from nonliving organic matter. For instance, many types of oomycetes grow on dead animals or algae. Saprobic protists have the essential function of returning inorganic nutrients to the soil and water. This process allows for new plant growth, which in turn generates sustenance for other organisms along the food chain. Indeed, without saprobic species, such as protists, fungi, and bacteria, life would cease to exist as all organic carbon became “tied up” in dead organisms.