21 PROKARYOTES AND VIRUSES

West Nile Virus Takes Off

In 336 B.C., when he was twenty years old, Alexander the Great ascended to the throne of Macedonia (Figure 21.1). During his reign, he carved out an empire that stretched across the Middle East and into northern India. He died twelve years later after he entered Babylon, the site of modern-day Baghdad.

According to one recorded account, a flock of ravens announced Alexander's arrival in the city. The birds behaved strangely, and some fell dead at his feet. Soon thereafter, Alexander became bedridden with severe back pain. Fever and chills, weakness, delirium, and paralysis followed, and then death.

An infectious disease expert, Charles Calisher, and epidemiologist John Marr connected the dots between the birds' behavior and Alexander's recorded symptoms. As they hypothesize, Alexander died as an outcome of *West Nile encephalitis*. A flavivirus, first isolated in 1937, causes this disease, which results in severe inflammation of the brain. Researchers had already discovered that the virus was once prevalent in Africa, West Asia, and the Middle East. Was there an outbreak of West Nile encephalitis during Alexander's time? Possibly.

Until the summer of 1999, no one knew that the virus had entered the Western Hemisphere. Then people in and around New York City started wondering about the dead and dying crows—and the mysteriously sickened horses and humans. West Nile virus particles turned up in tissue samples from infected individuals. Sixty-two people became ill that summer. Seven died.

The virus hitchhiked, inside infected birds, across North and Central America. By 2003, nearly 9,000 human cases of West Nile encephalitis or fevers had been reported; and more than 200 people had died. Cases popped up in every state except Maine, Washington, and Oregon. Canada and the Cayman Islands reported cases as well. Birds and horses in Mexico showed signs of infection. Most likely, the virus will become distributed through all of the Americas.

West Nile virus clearly is pathogenic. A **pathogen** is an infectious, disease-causing agent that can infect a host organism and multiply in or on it. Disease follows when metabolic activities of its descendants damage tissues and interfere with how the host body works.

As far as we know, you can't "catch" West Nile virus from a dog, a cat, or a classmate. Like other flaviviruses, this one typically travels inside mosquitoes. The insects pick up virus particles that are circulating in a host's blood. After sucking blood from one host, they can infect a new host when they draw blood from it. In North America, at least forty-three different kinds of mosquitoes have now become vectors for West Nile virus.

Figure 21.1 A clue to viral history? Alexander the Great may have died of West Nile encephalitis. Ravens and crows are highly susceptible to this viral disease. Today, biologists are monitoring these birds to assess the spread of the disease through North, Central, and South America.

IMPACTS, ISSUES

Infections may have widespread ecological impact. In North America, the virus has been detected in more than 150 kinds of birds and mammals, and in alligators. Many animals infected by the virus do not get sick. In effect, they are reservoirs for the virus, and they can transmit them to vulnerable hosts. If members of an endangered species can become hosts, they may push the species toward extinction.

This chapter can start you thinking about the microbes, the unseen multitudes at the boundary between nonliving and living things. Viruses hover near the boundary, and prokaryotes are just inside it. Most of us tend to judge the microbes through the prism of human interests. We find many of them dangerous, others beneficial, and the vast majority seemingly of no concern to us. However, in the evolutionary view, they simply are going about the business of surviving and making copies of themselves—and their lineages have been doing so for far longer than ours.

How Would You Vote?

Eliminating mosquitoes is the best defense against West Nile virus. Many local agencies are spraying pesticides wherever mosquitoes are likely to breed. Some people fear ecological disruptions and bad effects on health, and say spraying will never get rid of all mosquitoes anyway. Would you support a spraying program in your community? See BiologyNow for details, then vote online.

Key Concepts

DISTINCTLY PROKARYOTIC FEATURES

In structural terms, prokaryotic cells are the simplest forms of life; they do not have a profusion of internal, membrane-bound organelles, as eukaryotic cells do. Collectively, they show great metabolic diversity. Section 21.1

HOW PROKARYOTIC CELLS REPRODUCE

Prokaryotic cells reproduce by prokaryotic fission. This cell division mechanism starts with DNA replication. Deposits of new membrane and wall material cut the cell in two. Some species transfer genes by conjugation. Section 21.2

BACTERIAL AND ARCHAEAN LINEAGES

Researchers are clarifying relationships among prokaryotes. Bacteria are the most ancient cells. Archaeans resemble prokaryotes and eukaryotes. Sections 21.3–21.5

BASIC FEATURES OF VIRUSES

A virus is a noncellular infectious particle with DNA or RNA, a protein coat, a few enzymes, and in some cases an outer envelope. A virus cannot replicate itself without pirating the metabolic machinery of a specific host cell. Section 21.6

HOW VIRUSES ARE REPLICATED

Viral multiplication cycles involve attachment to a host cell, penetration of its plasma membrane, replication of the viral DNA or RNA and synthesis of viral proteins, assembly of viral particles, and release from the host cell. Section 21.7

THE BAD BUNCH

Humans are hosts to diverse pathogens and parasites. In evolutionary terms, the pathogen or parasite that leaves the most descendants wins. This happens when the survival of a coevolved host species is not threatened. Section 21.8

Links to Earlier Concepts

This chapter picks up where Section 4.3, the introduction to prokaryotic cells, left off. It zeros in on the bacterial and archaean branches of the tree of life (19.5). You will be drawing on the theories of the physical and chemical conditions under which life originated (20.1–20.3).

You may wish to reflect on the definitions of photoautotrophs, chemoautotrophs, and heterotrophs (Chapter 7 introduction and Section 7.8). You will be making a distinction between prokaryotic and eukaryotic cell division mechanisms (10.6). You also will consider how prokaryotes transfer genes by way of those plasmids you read about earlier (16.1).

21.1 Characteristics of Prokaryotic Cells

LINKS TO SECTIONS 4.3, 5.5, 7.8, 8.5

Of all organisms, prokaryotic cells are the smallest and the most far-flung, abundant, and metabolically diverse. Deserts, hot springs, glaciers, the seafloor, and rocks 2,800 meters below Earth's surface are home to different kinds. Billions live in a handful of rich soil. The ones living in your gut and on your skin outnumber your body cells!

Prokaryotes are the most ancient lineages. Trace any line of descent back far enough and you find ancestral prokaryotes. From *Escherichia coli* to clams, elephants, and redwoods, all of life interconnects, regardless of evolutionary distance.

Recall, from Section 4.3, that "prokaryotic" means these cells originated before the kinds with a nucleus. Membrane-bound, internal sacs of any kind are rare; metabolic reactions occur at the plasma membrane or in the cytoplasm. But structural simplicity does not mean that prokaryotic cells are inferior to eukaryotic cells. Being tiny, fast reproducers, they survive very well without great internal complexity. Table 21.1 and Figure 21.2 present their basic characteristics.

Table 21.1 Characteristics of Prokaryotic Cells

1. No membrane-bound nucleus.
2. Generally a single chromosome (a circular DNA molecule); many species also contain plasmids.
3. Cell wall present in most species.
4. Reproduction mainly by prokaryotic fission.
5. Collectively, great metabolic diversity among species.

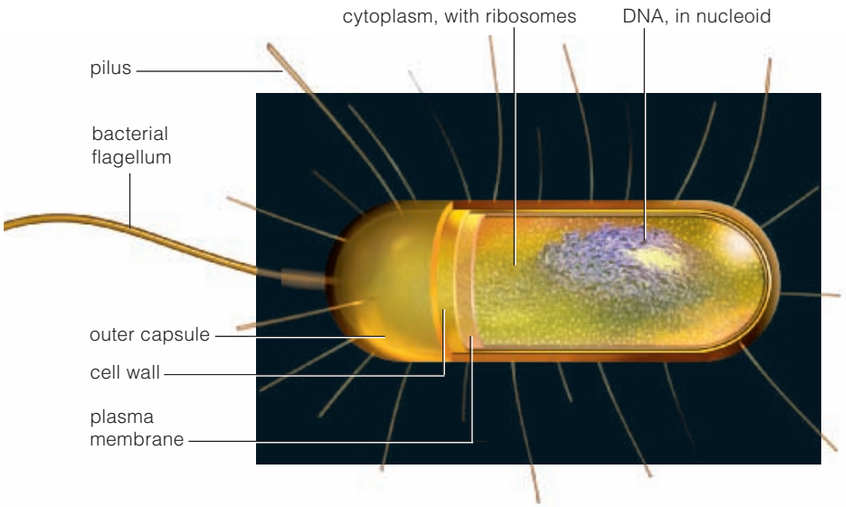


Figure 21.2 ***Animated!*** Generalized prokaryotic cell.

SIZES AND SHAPES

By now you have a sense of the microscopically small sizes of prokaryotic cells. Their width and length are between 0.5 and 1 micrometer, on the average. A few species are as large as 10 micrometers.

Three basic shapes are common among them. A spherical shape is a **coccus** (plural, cocci; from a word meaning berries). A rod shape is a **bacillus** (plural, bacilli, meaning small staffs). A cell body having one or more twists is called a **spirillum** (plural, spirilla):

Figure 21.3 shows examples of these shapes, but there are variations on the basic plan. Cocci may be oval or flattened. Bacilli may be long and thin or tapered like a cigar. Some spiral species are curled like a comma or a corkscrew (Figure 19.15). Extensions give some species a star shape, and one archaean looks a bit like a postage stamp. Also, when cells are dividing, the daughter cells often stick together in chains, sheets, or other aggregations, as in Figure 21.3*b*.

STRUCTURAL FEATURES

For most prokaryotic species, a **cell wall** encloses the plasma membrane (Figure 21.2). This somewhat rigid, permeable structure helps the cell maintain its shape and resist rupturing when the internal fluid pressure increases, as Section 5.5 explains. Unlike the cell wall of archaeans and some eukaryotic species, a bacterial wall consists of peptidoglycan, a unique compound in which peptide bonds crosslink many polysaccharide strands to one another.

When doctors must diagnose an infectious disease, they may use **Gram staining**. This procedure can help identify many bacterial species by their wall staining properties. The unknown species is exposed to purple dye, then iodine, then an alcohol wash, and finally a counterstain. The wall of *Gram-positive* species stays purple. The wall of *Gram-negative* species loses color at first, but the counterstain turns it pink (Figure 21.4).

A sticky mesh, or **glycocalyx**, often encloses the cell wall. It consists of polysaccharides, polypeptides, or both. When highly organized and attached firmly to the wall, it forms a capsule. When less organized and loosely attached, it forms a slime layer. The mesh helps the cell attach to teeth, mucous membranes of the intestinal or vaginal wall, rocks in streambeds, and other interesting surfaces. It helps some encapsulated

types resist being engulfed by phagocytic, infection-fighting cells of a host organism.

Many species have one or more **bacterial flagella** (Figure 14.6*a*). Unlike eukaryotic flagella, these motile structures do not have microtubules, and they do not bend side to side. Instead, they rotate like a propeller. Also, **pili** (singular, pilus) are common. These are thin, filamentous proteins that project above the cell wall, as in Figure 21.3*c*,*d*. Some pili help the cell adhere to surfaces. A kind called a sex pilus helps one cell pull another cell next to it as a prelude to conjugation, an interaction explained in the next section.

METABOLIC DIVERSITY

Remember the Chapter 7 introduction? All organisms must acquire energy and carbon. Compared to other organisms, however, the prokaryotic cells collectively show the most diversity in how they get it.

Like plants, *photoautotrophic* prokaryotes are self-feeders that make their own food by photosynthesis. Cyanobacteria are like chloroplasts. They get electrons and hydrogen for the reactions from water molecules and release free oxygen as a product. Light-trapping pigments and electron transfer chains are embedded in their plasma membrane. Different photoautotrophs are strict anaerobes; free oxygen kills them. They get the electrons and hydrogen from gaseous hydrogen, hydrogen sulfide, and other inorganic compounds.

There also are self-feeding *chemoautotrophic* species. They obtain carbon from CO_2, and they obtain energy by oxidizing organic or inorganic compounds, such as iron and sulfur (Section 7.8).

Photoheterotrophic prokaryotes are not self-feeders. They tap the sun's energy—but they must get carbon from organic compounds. *Chemoheterotrophic* species are by far the most common types, and they are not self-feeders, either. The parasites get nutrients from a living host. The saprobes, like fungi, digest organic products or remains of organisms in the environment, then absorb the breakdown products.

Nearly all prokaryotic cells are microscopic in size. Unlike eukaryotic cells, they do not have great internal complexity, nor do they require it. Most have a cell wall that often is enclosed in a capsule or slime layer. The bacterial cell wall is uniquely made of peptidoglycan.

Surface specializations include bacterial flagella and pili.

Collectively, prokaryotic cells show the most diversity in acquiring energy and carbon building blocks.

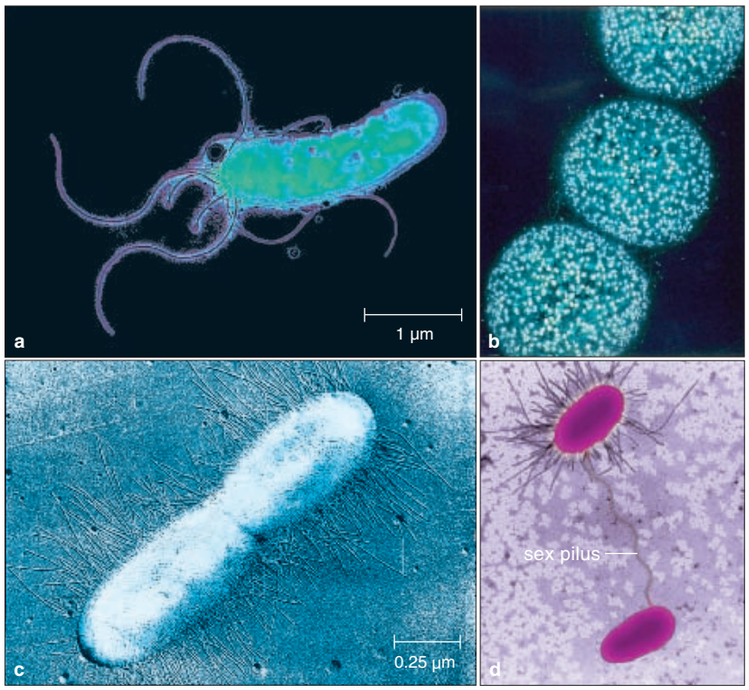


Figure 21.3 A few prokaryotic cell shapes and structures. (**a**) *Helicobacter pylori*, with a tuft of flagella. This pathogen can colonize the stomach lining. Untreated infections invite gastritis, peptic ulcers, and possibly stomach cancer. *H. pylori* can contaminate water and food, especially unpasteurized milk. A combination of antibiotics and an antacid kills it. (**b**) *Thiomargarita namibiensis*, a bacterial cell visible to the naked eye. A nitrate-filled vacuole occupies most of its cytoplasm. (**c**) An *Escherichia coli* cell, with its profusion of pili. This cell is dividing. (**d**) Sex pilus reeling in an *E. coli* cell (lower right) to the cell above, which will then transfer genetic material to it.

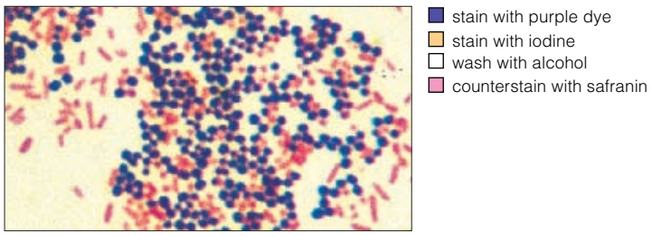


Figure 21.4 Gram staining. Cocci and bacilli smeared on a slide were stained with a purple dye (such as crystal violet), washed, and stained with iodine. Staining turned all of the cell walls purple. The slide was then washed with alcohol, which removed the stain from the Gram-negative cells and made them colorless.

Next, the slide was counterstained (with safranin), washed, and dried. The Gram-positive cells (here, *Staphylococcus aureus*) stayed purple. However, the counterstain tinted the Gram-negative cells (*E. coli*) light pink.

21.2 Prokaryotic Growth and Reproduction

LINKS TO SECTIONS 10.6, 16.1

Compared to eukaryotic cells (Section 10.6), prokaryotic cells divide by a more straightforward mechanism.

THE NATURE OF GROWTH

Prokaryotic cells grow by increasing their component parts between divisions. We measure **growth** in terms of increases in size for large, multicelled organisms, but doing so for a microscopically small cell would be a bit pointless. Instead, we measure the growth of any prokaryotic species in terms of increases in the number of cells in its populations. Under ideal conditions, a prokaryotic cell divides in two, then division of two cells results in four cells, four result in eight, and so on. Many types can divide every half hour; a few can do so every ten or twenty minutes. Such rates of increase can result in large population sizes in short order.

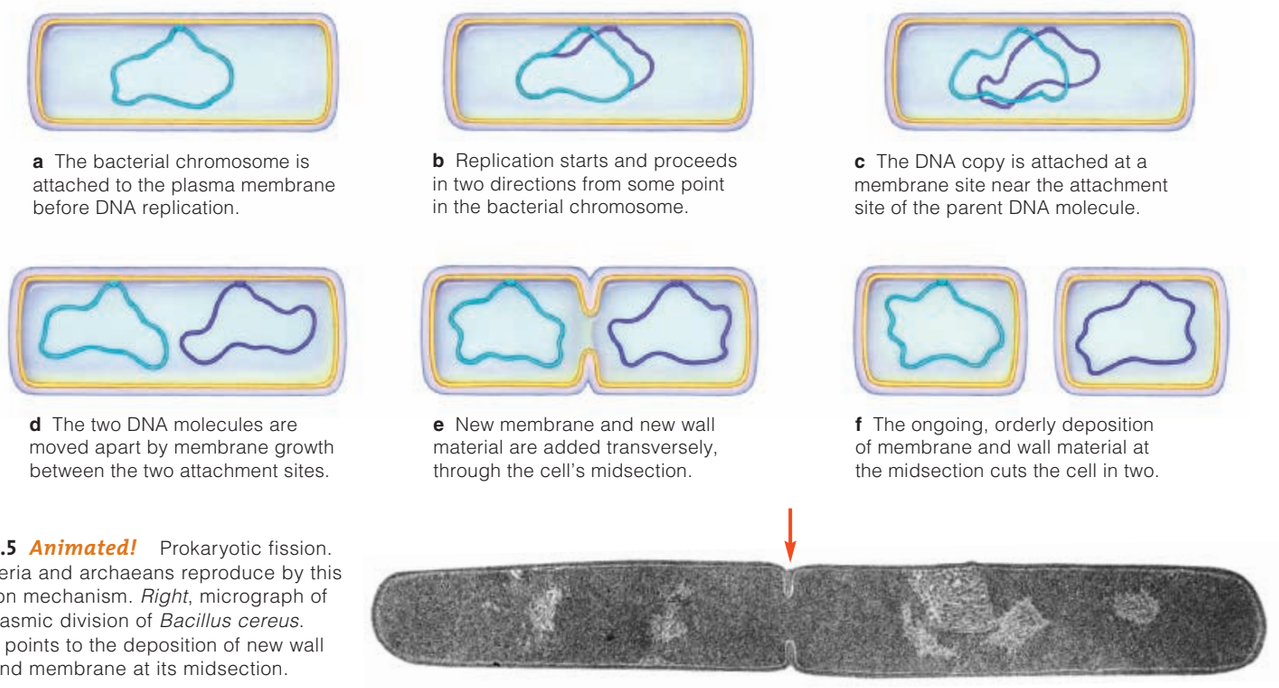
Some cells reproduce rarely, but their populations grow where no others can. This is the case for the few species clinging to life in Antarctic glaciers, the Negev Desert, and deep in Earth's crust. Even K–12, a strain of *E. coli* originally isolated from the human gut, has been cultivated for such a long time in the laboratory that it no longer can grow when reintroduced into its natural habitat. As an outcome of microevolutionary processes, it has become adapted to the conditions in its artificial laboratory environment.

PROKARYOTIC FISSION

A prokaryotic cell nearly doubles in size, then divides in two. Each daughter cell inherits a single **bacterial chromosome**—a circularized, double-stranded DNA molecule that has a few proteins associated with it. In some species, the daughter cell merely buds from the parent cell. Most often, however, a cell reproduces by a division mechanism called **prokaryotic fission**.

Prokaryotic fission starts when a cell replicates its DNA (Figure 21.5). The parent molecule and the copy are both anchored to the plasma membrane at adjacent sites. Meanwhile, the cell is synthesizing proteins and lipids, which become added to the plasma membrane between the two attachment sites. The additions make the membrane grow, which moves the molecules of DNA apart. New wall material is deposited onto the growing membrane, and growth continues on through the cell midsection. It cuts the cytoplasm in two, the result being two genetically equivalent daughter cells.

Especially in microbiology, you may hear someone refer to this division mechanism as *binary* fission, but such usage might be confusing. The same term applies to an asexual reproductive mode among flatworms and some other animals. It refers to growth by mitotic cell divisions, then division of the whole body into two parts of the same or different sizes.



a The bacterial chromosome is attached to the plasma membrane before DNA replication.

b Replication starts and proceeds in two directions from some point in the bacterial chromosome.

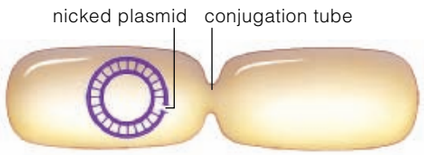
c The DNA copy is attached at a membrane site near the attachment site of the parent DNA molecule.

d The two DNA molecules are moved apart by membrane growth between the two attachment sites.

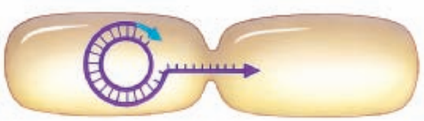
e New membrane and new wall material are added transversely, through the cell's midsection.

f The ongoing, orderly deposition of membrane and wall material at the midsection cuts the cell in two.

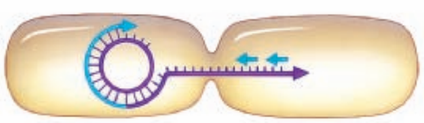
Figure 21.5 ***Animated!*** Prokaryotic fission. Only bacteria and archaeans reproduce by this cell division mechanism. *Right*, micrograph of the cytoplasmic division of *Bacillus cereus*. The arrow points to the deposition of new wall material and membrane at its midsection.



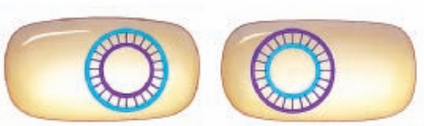
a A conjugation tube has already formed between a donor and a recipient cell. An enzyme has nicked the donor's plasmid.



b DNA replication starts on the nicked plasmid. The displaced DNA strand moves through the tube and enters the recipient cell.



c In the recipient cell, replication starts on the transferred DNA.



d The cells separate from each other; the plasmids circularize.

Figure 21.6 ***Animated!*** Conjugation between two prokaryotic cells. For clarity, the plasmid's size has been greatly increased and the chromosome is not shown.

CONJUGATION BETWEEN CELLS

Salmonella, *Streptococcus*, and *E. coli* and other species also inherit plasmids. As you know, each **plasmid** is a small, self-replicating circle of DNA with a few genes (Section 16.1). An F (*F*ertility) plasmid has genes that confer the means to engage in a form of **conjugation**. A donor cell transfers plasmid DNA to a recipient cell. Such transfers have been noted between *E. coli* and yeast cells in the laboratory. The F plasmid contains instructions for making a sex pilus (Figure 21.3*d*). Sex pili at a donor cell's surface can hook onto a recipient cell and pull it next to the donor. Shortly after the two cells make contact, a tiny conjugation tube develops between them. After this, plasmid DNA is transferred through the tube, in the manner shown in Figure 21.6.

Only bacteria and archaeans reproduce by a cell division mechanism, prokaryotic fission, that follows replication of DNA. Each daughter cell inherits one DNA molecule (one chromosome). Many species also transfer plasmid DNA.

21.3 Classifying Prokaryotes

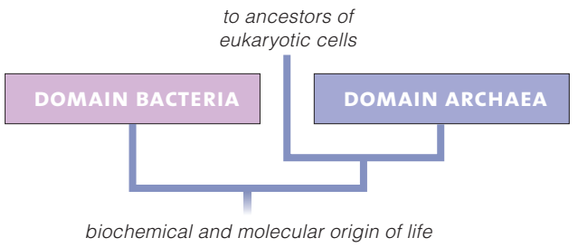
How can we classify prokaryotes? Except for stromatolites, the most ancient groups are not well represented in the fossil record. Most are not represented at all.

LINKS TO SECTIONS 1.4, 16.1, 16.2, 19.5

Traditionally, prokaryotes have been classified mainly by **numerical taxonomy**. An unidentified prokaryotic cell is compared against a known group on the basis of shape, motility, wall staining attributes, nutritional requirements, metabolism, and other traits. The more traits that the cell shares with the known group, the closer is their inferred relatedness.

Automated gene sequencing and other methods of comparative biochemistry are clarifying phylogenies (Sections 16.2 and 16.3). The comparisons of ribosomal RNAs are especially revealing. As you will read soon, mutations that accumulated in the rRNAs of different prokaryotic lineages are being measured directly.

Biochemical analyses are uniting some groups that did not seem to be related on the basis of other tests. As Section 19.5 explains, they revealed the first genetic divergence that occurred shortly after life originated. One branching led to **Bacteria**. The other gave rise to **Archaea** and to the ancestors of eukaryotic cells:



By now, you probably have sensed that *species* is the basic unit in prokaryotic classification schemes. Even so, the definition that fits sexually reproducing species does not fit prokaryotes, which are not reproductively isolated populations of interbreeding individuals. A prokaryotic cell generally does its own thing. Also, many variations that do show up among species are determined by relatively few genes. If two cells under study show minor differences, one of them might be classified as a **strain**, not a new species. The next two sections take these considerations into account in their listings of major groups.

Prokaryotic cells are now being classified on the basis of biochemical comparisons as well as numerical taxonomy, or the total percentage of observable traits they have in common with a known prokaryotic group.

21.4 Domain Bacteria

LINKS TO SECTIONS 7.8, 16.7 20.1–20.3

Figure 21.7 shows which of the many thousands of bacterial groups we sample throughout this book.

REPRESENTATIVE DIVERSITY

Bacteria originated when unstable crustal plates were colliding and forming the proto-continents. Volcanoes were spewing lava into superheated water and venting gases into a steaming atmosphere that big meteorites repeatedly pierced. For the next 3 billion years, cells did not change much, except in their metabolism. The first kinds may have resembled *Aquifex aeolicus*, one of the most extreme thermophilic species known (Figure 21.7). This one lives in water as hot as 96°C (204.8°F).

Cyanobacteria were ancient species (Section 20.3). Like their modern descendants, they released oxygen during photosynthesis. Collectively, these cells and the chloroplasts descended from them probably account for most of the free oxygen in the atmosphere. Today, cyanobacteria also cycle considerable carbon, oxygen, nitrogen, and other nutrients through aquatic habitats and soils. A few are symbionts with fungi, in lichens.

After mitotic cell division, daughter cyanobacterial cells often remain attached as mucus-sheathed chains that form slimy mats (Figure 21.8*a*,*b*). When nitrogen is scarce, some cells in chains of *Anabaena* develop into heterocysts, which convert nitrogen gas to ammonia. Ammonia dissolves at once into a form that can be used to synthesize nitrogen compounds. Heterocysts share the compounds with other cells in the chain and get carbohydrates in return. Cyanobacterial species are notable specialists in nitrogen fixation.

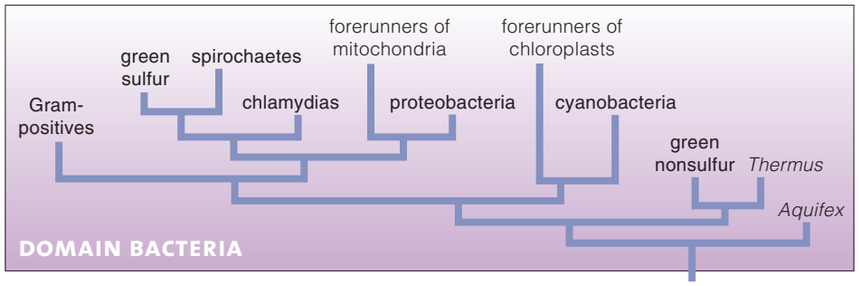
Proteobacteria are the most diverse monophyletic group of bacteria. They are all Gram-negative species; staining tints their walls pink. *Chromatium* species are anaerobic photosynthesizers. Their bacteriochlorophyll pigments are structurally similar to chlorophylls but have a slightly different absorption spectra.

Many proteobacteria are important nutrient cyclers. *T. namibiensis* helps connect sulfur and nitrogen cycles in the seas. It strips electrons from sulfur compounds as an energy source and also stores nitrate for use as a final electron acceptor. *Rhizobium* in the roots of peas and many other legumes fixes nitrogen. *Agrobacterium tumefaciens* causes tumors in plants but it also is a fine vector for genetic engineering (Section 16.7).

Make note of the genus names in Figure 21.7. You already met some of these pathogenic proteobacteria in earlier chapters and will encounter the rest later on.

Chlamydia is a group of intracellular parasites that cannot make ATP; they pilfer it from animal cells. One species causes a sexually transmitted disease you will read about in Section 44.8. **Spirochaetes** are free-living cells, parasites, or symbionts. All are motile. All look like stretched-out springs (Figure 21.8*c*). Symbionts, including *Pillotina* and others, in the termite gut digest cellulose in wood. *Borrelia burgdorferi* travels in ticks that bite many wild animals and humans. In humans, this spirochaete infection results in Lyme disease, a focus of Section 25.16.

Gram-positives are still being sorted out; they are not a monophyletic group. Staining



Gram-positives (not a monophyletic group)	*Actinomyces, Clostridium, Bacillus, Lactobacillus, Listeria, Streptomyces, Heliobacterium, Mycobacterium, Mycoplasma, Propionibacterium, Streptococcus*
Chlamydia	*Chlamydia*
Spirochaetes	*Borrelia, Pillotina, Spirillum, Treponema*
Green sulfur bacteria	*Chlorobium*
Proteobacteria (Gram-negative)	*Agrobacterium, Azospirillum, Azotobacter, Campylobacter, Chromatium, Escherichia, Haemophilia, Myxococcus, Helicobacter, Neisseria,Nitrobacter, Rickettsia, Pseudomonas, Rhizobium, Salmonella, Shigella, Thiomargarita, Vibrio, Yersinia*
Cyanobacteria	*Anabaena, Nostoc, Oscillatoria*
Deinococcus	*Thermus*
Green nonsulfur bacteria	*Chloroflexus*
Aquificales	*Aquifex (most deeply branching group)*

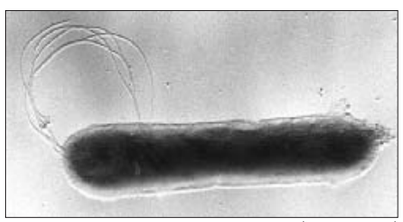


Figure 21.7 Domain Bacteria. This evolutionary tree is by no means inclusive. It is meant only to convey some relationships among the prokaryotic groups mentioned in this book. *Above*, micrograph of *Aquifex aeolicus*, a descendant of what may be one of the earliest bacterial lineages.

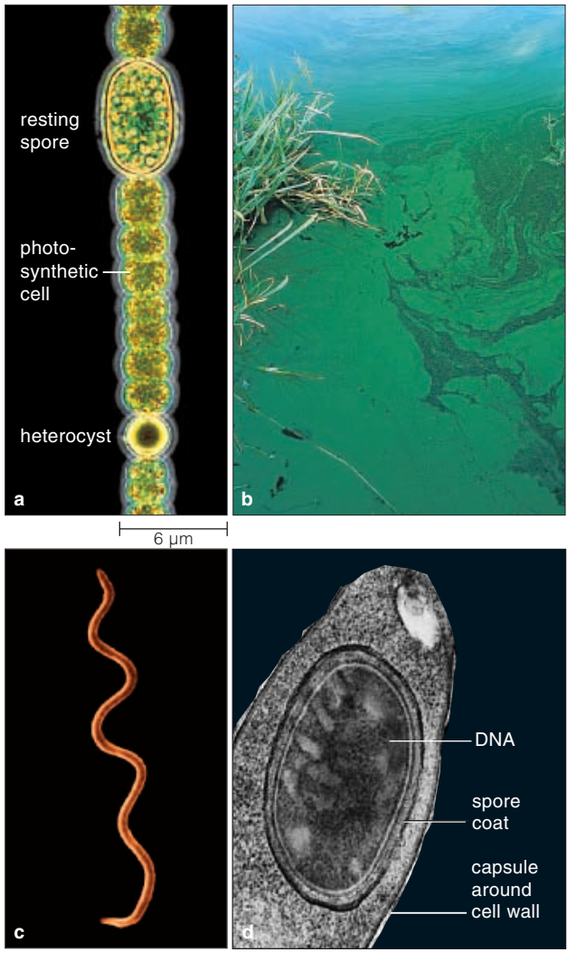


Figure 21.8 A few bacteria. (**a**) An *Anabaena* chain with a resting spore and a heterocyst. (**b**) Cyanobacterial chains forming a mat on a nutrient-rich pond surface. (**c**) *Borrelia burgdorferi*, a spirochete that causes Lyme disease in humans. (**d**) Endospore forming in *Clostridium tetani.*

tints their multilayered wall purple. Most species are chemoheterotrophs. We use the fermenting activities of *Lactobacillus* species to make many popular foods, including yogurt. *L. acidophilus* lowers the pH of skin and of intestinal and vaginal linings, which helps keep pathogenic bacteria and fungi from forming colonies.

The Gram-positive bacteria *Clostridium* and *Bacillus* make **endospores**. This resting structure encloses the bacterial chromosome and a bit of cytoplasm (Figure 21.8*d*). It can resist heat, irradiation, drying out, acids, disinfectants, and boiling water. It germinates when conditions favor growth. A bacterium emerges from it, and normal metabolic function resumes.

Endospores do damage inside the human body. In 2001, someone slipped *Bacillus anthracis* endospores into envelopes and mailed them. A few people opened the mail, breathed in endospores, and died of anthrax. *Clostridium tetani* endospores that slip inside the body through cuts or wounds can cause tetanus, a disease described in Section 37.9. *C. botulinum* endospores can taint canned food. Toxins synthesized by bacteria that emerge from germinating endospores cause botulism, a dangerous form of food poisoning.

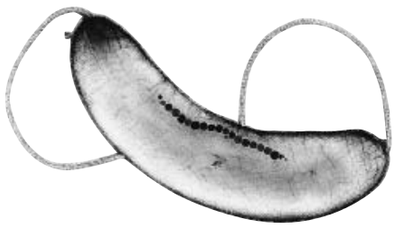


Figure 21.9 Magnetotactic bacterium. Inside the cytoplasm is a chain of magnetite particles that acts like a compass as the cell moves.

REGARDING THE "SIMPLE" BACTERIA

Bacteria are small. Their insides are not elaborate. *But bacteria are not simple.* They sense and move toward areas where nutrients are more plentiful and where other conditions also favor growth. Aerobes move to oxygen; anaerobes move away from it. Photosynthetic types move toward light but away from light that is too intense. Many species avoid toxins or predators.

Magnetotactic bacteria migrate in the ocean, and they grow best in oxygen-poor seawater. They contain a compass—chains of magnetic particles that respond to Earth's magnetic field (Figure 21.9). For instance, in the Northern Hemisphere, geomagnetic north points downward at a slight angle from the equator toward the North Pole. Cells responding to the angle move farther down from the surface waters, where oxygen concentrations are not as great.

Some bacteria show a collective behavior, as when millions of free-living myxobacteria cells glide about as a "predatory" colony. They secrete enzymes that digest "prey," such as other bacteria. They move and change direction as a unit when following chemical gradients toward food. When food dwindles, many of the cells mass together, interact chemically, and form spore-bearing structures. Some cells differentiate and form a stalk; others form branching stalks or clusters of spores. Each spore holds a single, living cell that can germinate and give rise to a new colony.

Domain bacteria is the most ancient lineage of prokaryotic cells. Its groups include photoautotrophs, chemoautotrophs that cycle nutrients in habitats, and chemoheterotrophs. The chemoheterotrophs are most diverse; many species are dangerous parasites and pathogens.

21.5 Archaeans

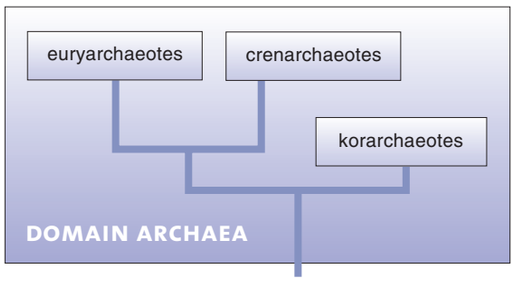
LINKS TO SECTIONS 4.3, 7.8, 8.5, 16.2, 19.5

Archaeans are prokaryotic, but in some respects they are as similar to eukaryotes as they are to bacteria. New species are turning up almost everywhere.

THE THIRD DOMAIN

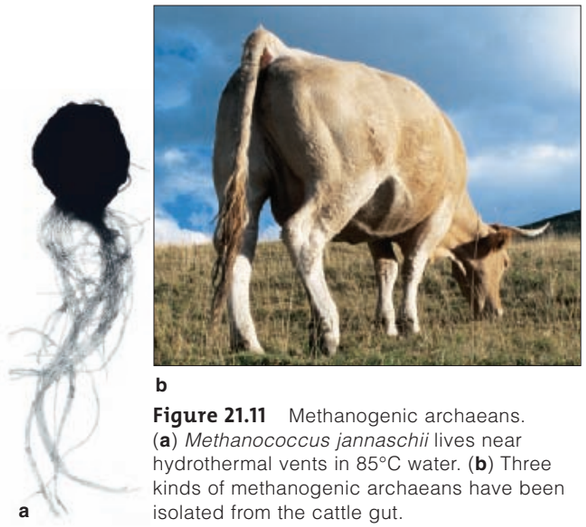
It is easy to see why all prokaryotes were once placed in a single kingdom. As sketched out in Section 4.3, archaeans resemble bacteria in size and shape, and in not having a nucleus. They all have operons and other shared features. But archaean cell walls are different. Their membrane phospholipids are mirror images of those in bacterial membranes, and different enzymes make them. Also, the archaeans resemble eukaryotes in several ways. For instance, they, too, make histones. They make the same codon (methionine) to start gene transcription; bacteria make formylmethionine. Their RNA polymerases and some transcription factors are more eukaryotic than prokaryotic.

By the 1970s a molecular biologist, Carl Woese, was comparing the ribosomal RNAs of prokaryotes. The genes for rRNA are essential for protein synthesis, yet some of their base sequences have mutated without compromising rRNA's function. Many slight changes have accumulated in rRNAs of different lineages and can be measured directly. To Woese's great surprise, many lineages turned out to be somewhere *between* bacteria and eukaryotic cells in genetic distances! He proposed that the six-kingdom classification system be subsumed into three domains (Section 19.5).



Euryarchaeotes	Methanogens, extreme halophiles, sulfate reducers, unwalled archaeans (e.g.,*Methanococcus, Thermoplasma, Methanobacterium, Halobacterium*)
Crenarchaeotes	Extreme thermophiles, marine cryophiles (e.g., *Thermoproteus, Sulfolobus*)
Korarchaeotes	Newly discovered extreme thermophiles

Figure 21.10 The major groups of Domain Archaea. A few of the known representatives are listed.



a **b**

Figure 21.11 Methanogenic archaeans. (**a**) *Methanococcus jannaschii* lives near hydrothermal vents in 85°C water. (**b**) Three kinds of methanogenic archaeans have been isolated from the cattle gut.

Today there is wide acceptance that archaeans form a "third" domain, with lineages that may not have changed much since life originated (*archae–* means ancient). Based on ongoing comparisons, the domain already has been subdivided into three major groups. They are Euryarchaeota, Crenarchaeota, and the more recently discovered Korarchaeota (Figure 21.10).

HERE, THERE, EVERYWHERE

With respect to physiology, most of the archaeans are **methanogens** (methane makers), **extreme halophiles** (salt lovers), and **extreme thermophiles** (heat lovers). Methanogens and halophiles are euryarchaeotes. Most of the domain's thermophiles are crenarchaeotes.

The three informal designations can be confusing, because many bacteria also are methanogens, extreme halophiles, and extreme thermophiles. Even so, they will persist. Why? Taxonomists might be pleased with the formal names they bestowed upon the three sets of archaeans, but students would have an easier time learning names that are less of a mouthful.

You read about the methanogenic archaeans at the start of Chapter 3. Different kinds have been found in marshes, Antarctica, the ocean, and deep in the Earth. A few are symbionts in the gut of termites and some other animals (Figure 21.11). All are strict anaerobes; free oxygen kills them. When forming ATP, they strip electrons from hydrogen gas (H_2) or acetate. Carbon from CO_2 is the final electron acceptor, and methane (CH_4) forms as the product. Collectively, methanogens in both prokaryotic domains release about 2 billion tons of methane annually. They have major impact on the global cycling of carbon.

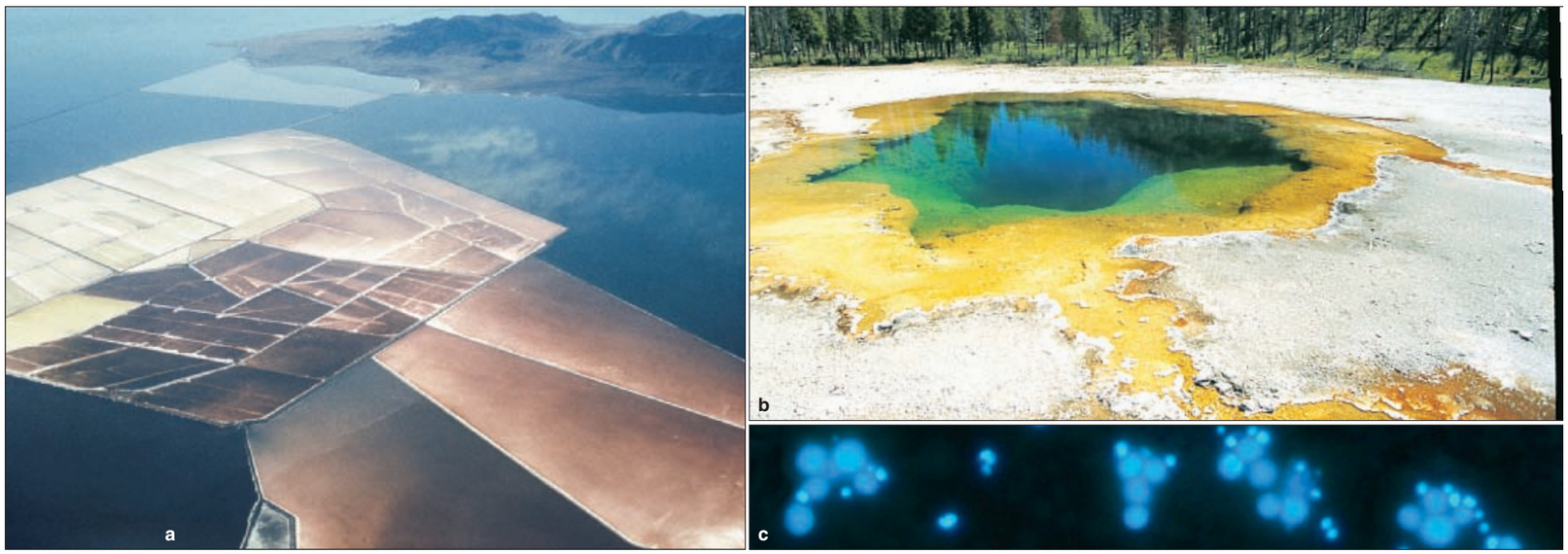


Figure 21.12 Life in extreme environments. (**a**) In salty evaporation ponds in Utah's Great Salt Lake, extreme halophiles (certain archaeans and red algae) tint the water pink. (**b**) Yellowstone's exceedingly hot springs and pools are among the habitats of many extreme thermophiles. (**c**) The parasitic *Nanoarchaeum equitans* (smaller *blue* spheres) grows only when attached to *Ignicoccus* (larger spheres). Both marine archaeans were isolated from 100°C water near a hydrothermal vent.

Extreme halophilic archaeans live in the Dead Sea, the Great Salt Lake, saltwater evaporation ponds, and other highly salty habitats (Figure 21.12*a*). Most get ATP by aerobic reactions but they can harness light energy when free oxygen is scarce. Bacteriorhodopsin is a unique light-activated pigment embedded in their plasma membrane. When it absorbs sunlight energy, it changes shape and pumps protons (H^+) out from the cell. H^+ flows back into it, through a type of ATP synthase, and drives ATP formation.

Extreme thermophilic archaeans also live in sulfur-rich hot springs (Figure 21.12*b*). Like methanogens, they are strict anaerobes. Unlike them, they use sulfur as an electron acceptor or donor in their ATP-forming reactions. *Sulfolobus* cells grow in acidic hot springs.

Other extreme thermophiles are the start of food webs near hydrothermal vents, where temperatures exceed 110°C. These archaeans use hydrogen sulfide escaping from the vents as an electron source for ATP-forming reactions. Their existence is cited as evidence that life could have originated on the seafloor.

Researchers came across *Nanoarchaeum equitans* as they were exploring hydrothermal vents near Iceland. At 400 nanometers across, this euryarchaeote is the smallest known cell and the only parasitic archaean (Figure 21.12*c*). At this writing, its genome has been sequenced. It is the smallest genome yet found.

Seawater samples collected from the depths off the coast of Antarctica and California hold more archaeans (mostly crenarchaeotes) than the bacteria in seawater near the surface. Some archaeans are as-yet unnamed cryophiles; they are adapted to temperatures below 15°C (59°F). Mounds of methane hydrate on the ocean floor and sediments from the Great Lakes contain archaeans. So do agricultural fields, natural grasslands, northern coniferous forests, and the Siberian tundra. Today, biologists are finding new species of archaeans almost everywhere, including inside the human gut.

Woese now compares the discovery of Archaea to the discovery of a continent, which he and others are exploring and mapping. They have come to recognize that these prokaryotes are diverse and widespread. They also have discovered that archaeans and bacteria in the same habitats swap genes, and may do so often.

Like bacteria, archaeans are prokaryotic cells, but in some respects they resemble eukaryotes. Enough differences have been identified at the molecular level to grant archaeans equivalent ranking with bacteria and eukaryotes.

Archaeans were once thought to be confined to extreme environments. Many are now being discovered alongside bacteria in more hospitable habitats.

21.6 The Viruses

LINKS TO SECTIONS 13.1, 13.2, 14.1

In ancient Rome, virus meant "poison" or "venomous secretion." In the late 1800s, this rather nasty word was bestowed on newly discovered pathogens, smaller than the bacteria being studied by Louis Pasteur and others. Many viruses deserve the name. They attack humans, cats, cattle, birds, insects, plants, fungi, protists, and bacteria. You name it, there are viruses that infect it.

DEFINING CHARACTERISTICS

Today, we define a **virus** as a noncellular infectious agent having two characteristics. First, a viral particle consists of a protein coat wrapped around a nucleic acid core—that is, its genetic material. Second, a virus cannot reproduce by itself. It can be reproduced only after its genetic material enters a host cell and directs that cell's biosynthetic machinery into making many copies of itself.

Different viruses contain DNA *or* RNA. Their coat consists of one or more types of protein monomers organized into a characteristic shape, such as a rod or polyhedron (with many sides), as in Figure 21.13. The coat protects the genetic material during the journey to a new host cell. It incorporates proteins that bind to specific receptors on host cells. Complex viruses have a sheath, tail fibers, and other structures attached to the coat. In some viruses, a bit of plasma membrane of an infected cell surrounds the coat when the virus particle buds off or when the membrane is ruptured. Glycoproteins spike above the membrane envelope.

The vertebrate immune system detects certain viral proteins. But genes for many viral proteins mutate at high frequencies, so viruses often elude the immune fighters. People susceptible to lung infections get new "flu shots" each year because the envelope spikes on influenza viruses keep changing.

EXAMPLES OF VIRUSES

Each kind of virus can multiply only in specific hosts. It cannot be studied easily except in cultures of living host cells. This is why much of our understanding of viruses comes from the **bacteriophages**, which infect bacterial cells. Unlike the cells of complex, multicelled species, bacterial hosts can be cultured easily and fast. Remember how bacteria and bacteriophages were used in early experimental studies of DNA (Section 13.1)? They are still used in genetic engineering.

Table 21.2 lists important groups of animal viruses. These viruses contain double- or single-stranded DNA or RNA, which gets replicated in various ways. Their sizes range from 18 nanometers (parvoviruses) to 350 nanometers (the brick-shaped poxviruses). Many cause diseases, including the common cold, certain cancers, warts, herpes, and influenza (Figure 21.14*a*,*b*). As you will see in Chapter 39, HIV is the trigger for AIDS. By destroying certain white blood cells, it weakens the immune system's ability to fight infections that may not otherwise be life threatening.

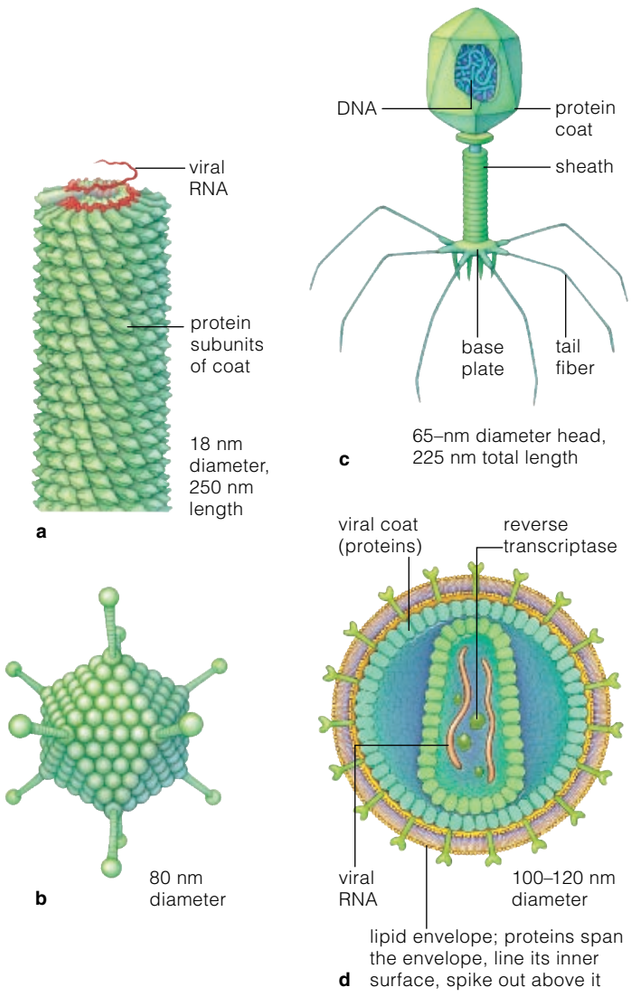


Figure 21.13 ***Animated!*** Structure of viruses. (**a**) *Helical* viruses, such as this tobacco mosaic virus, have a rod-shaped coat of protein subunits coiled helically around nucleic acid. (**b**) This adenovirus and other *polyhedral* viruses have a many-sided coat. (**c**) T-even bacteriophages and other *complex* viruses incorporate accessory parts attached to the coat. (**d**) Membrane encases the coat of the *enveloped* viruses. HIV, shown here, is an example.

Table 21.2 Classification of Some of the Major Animal Viruses

DNA Viruses	Some Diseases and Outcomes
Parvoviruses	Gastroenteritis; roseola (fever, rash) in small children; aggravation of symptoms of sickle-cell anemia
Adenoviruses	Respiratory infections (fever, cough, sore throat, rash), diarrhea in infants, conjunctivitis (inflamed, pebbly eye membranes); some cause tumors
Papovaviruses	Benign and malignant warts
Orthopoxviruses	Smallpox, cowpox, monkeypox
Herpesviruses:	
H. simplex type I	Oral herpes, cold sores
H. simplex type II	Genital herpes (Section 44.8)
Varicella–zoster	Chicken pox, shingles
Epstein–Barr	Infectious mononucleosis; cancers of skin, liver, cervix, pharynx; Burkitt's lymphoma (malignant tumor of jaw, face)
Cytomegalovirus	Hearing loss, mental impairment
Hepadnavirus	Hepatitis B (severe liver infection)
RNA Viruses	**Some Diseases and Outcomes**
Picornaviruses:	
Enteroviruses	Polio, hemorrhagic eye disease, hepatitis A (infectious hepatitis)
Rhinoviruses	Common cold
Hepatitis A virus	Inflammation of liver, kidneys, spleen
Togaviruses	Forms of encephalitis (inflammation in the brain), rubella
Flaviviruses	Yellow fever (fever, chills, jaundice), dengue (fever, severe muscle pain), St. Louis encephalitis
Coronaviruses	Upper respiratory infections, colds
Rhabdoviruses	Rabies, other animal diseases
Filoviruses	Hemorrhagic fevers, as by *Ebola* virus (Section 21.8)
Paramyxoviruses	Measles, mumps, respiratory ailments
Orthomyxoviruses	Influenza
Bunyaviruses	
Bunyamwera virus	California encephalitis
Phlebovirus	Hemorrhagic fever, encephalitis
Hantavirus	Hemorrhagic fever, kidney failure
Arenaviruses	Hemorrhagic fevers
Retroviruses:	
HTLV-I, HTLV-II*	Adult T-cell leukemia
HIV	AIDS
Reoviruses	Respiratory and intestinal infections

* Human T-cell leukemia virus.

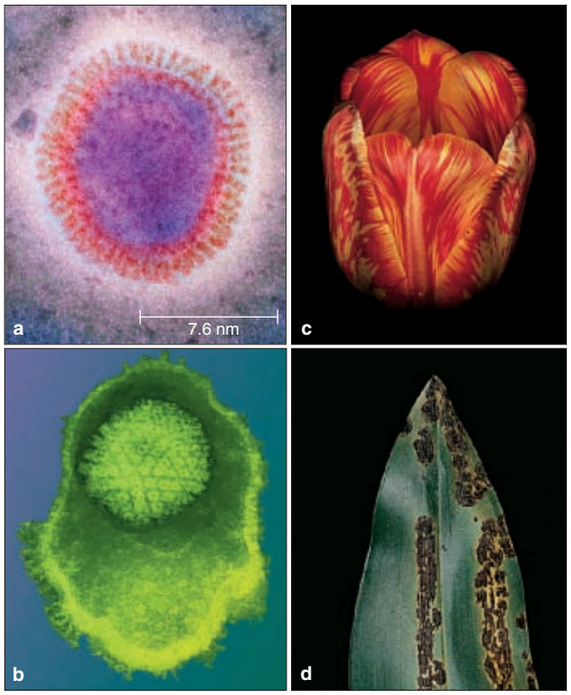


Figure 21.14 Examples of viruses and their effects. (**a**) Influenza virus. Spikes of glycoprotein project above its envelope. (**b**) One of the herpes viruses. Its envelope was pulled aside for this image. (**c**) Streaking in tulip petals. A harmless virus infected cells in the colorless parts and disrupted pigment formation. (**d**) An orchid leaf infected by a rhabdovirus.

Researchers who attempt to develop drugs against HIV and other diseases use HeLa cells and other cell lineages for initial experiments (Chapter 9). Later on, they must use laboratory animals, and then human volunteers, to test any potential drug for toxicity and effectiveness. Why? A functioning immune system is necessary to test responses to the drugs.

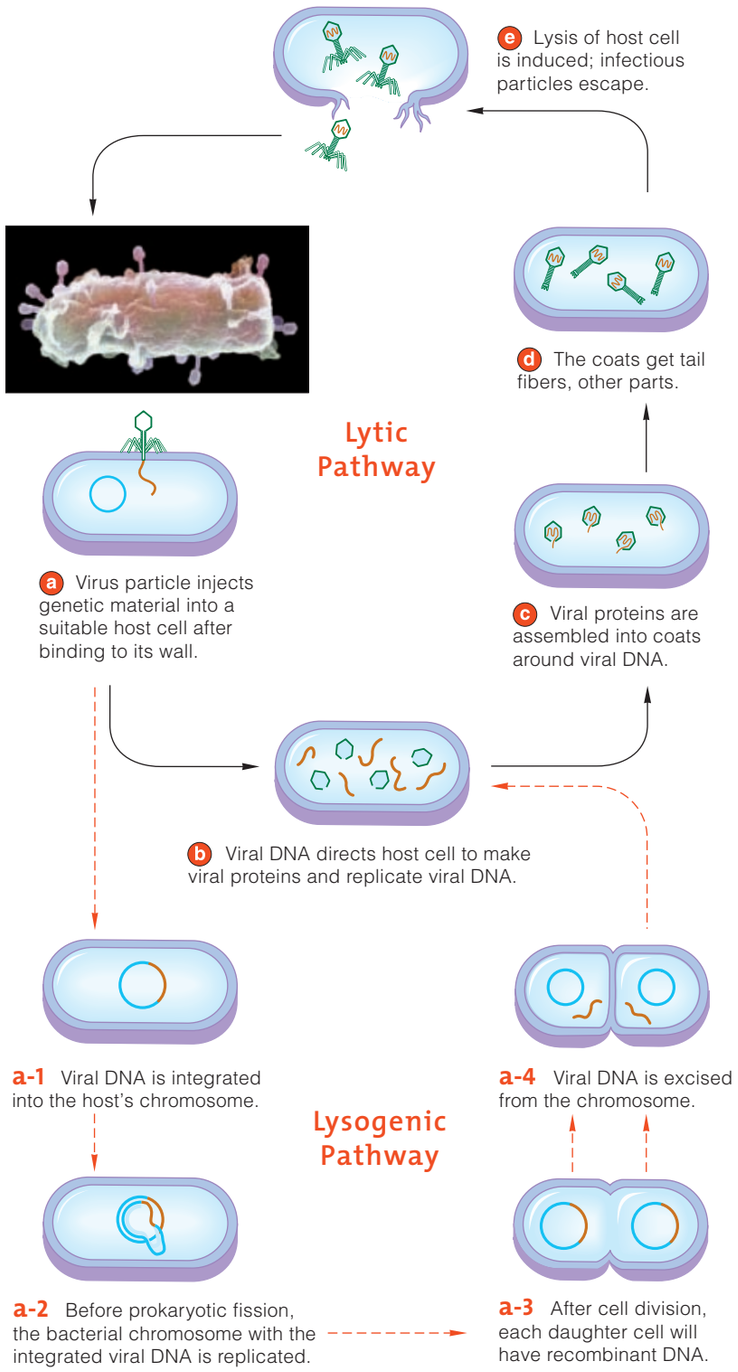
Plant viruses must breach plant cell walls to cause diseases. They typically hitch rides on the piercing or sucking devices of insects that feed on plant juices. Some RNA viruses infect tobacco plants (the tobacco mosaic virus), barley, potatoes, and other major crop plants. Certain DNA viruses infect such valued crops as cauliflower and corn. Figure 21.14*c,d* shows visible effects of two viral infections.

A virus is a noncellular infectious particle that consists of nucleic acid enclosed in a protein coat and sometimes an outer envelope. It cannot multiply without pirating the metabolic machinery of a specific type of host cell.

Nearly all organisms are targets of specific viruses.

21.7 Viral Multiplication Cycles

Even the simplest prokaryotes can replicate their own genetic material and reproduce. If we define life in terms of metabolism, protein synthesis mechanisms, and reproduction, then viruses are not alive. The catch is that they do contain DNA or RNA.



THE BASIC STEPS

Once different viruses infect host cells, they multiply in a variety of ways. Even so, nearly all multiplication cycles proceed through five steps, as outlined here:

1. *Attachment.* A virus particle attaches to a host cell by molecular groups that can chemically recognize and lock on to specific molecular groups of receptors at the cell surface.

2. *Penetration.* Either the virus particle or its genetic material alone crosses the plasma membrane of a host cell and enters the cytoplasm.

3. *Replication and then synthesis.* In an act of molecular piracy, the viral DNA or RNA directs the host cell's transcription and translation mechanisms into making many copies of viral nucleic acids and viral proteins, including enzymes.

4. *Assembly.* The viral nucleic acids and viral proteins become organized as new infectious particles.

5. *Release.* By one mechanism or another, the newly formed virus particles are released from the cell.

We can use the lytic and lysogenic pathways that are common among bacteriophage multiplication cycles to give you an idea of what happens in these steps.

Lytic Pathway In a **lytic pathway**, steps 1 through 4 proceed rapidly, and new particles are released when the host cell undergoes **lysis**. In this context, "lysis" means that the damage to a cell's plasma membrane, wall, or both is allowing the cytoplasm to dribble out. New virus particles escape while the ruptured cell is dying. Late into most lytic pathways, the host cell synthesizes a viral enzyme, and that enzyme's action triggers the cell's swift destruction (Figure 21.15).

Lysogenic Pathway During a **lysogenic pathway**, a latent period extends the duration of the cycle. In this case, the virus does not kill its host outright. Instead,

Figure 21.15 ***Animated!*** Generalized multiplication cycle for some bacteriophages. Virus particles may be produced and released by a lytic pathway. For certain viruses, the lytic pathway may expand to include a lysogenic pathway.

a viral enzyme cleaves the host's chromosomal DNA, then integrates the viral genes into its base sequence.

An infected cell may not divide for a while. When it does, it replicates its DNA, including all of the foreign genes in the recombinant molecule. As a result of one instance of genetic recombination, miniature time bombs are passed on to its descendants, and all of their descendants. At some point, however, a molecular signal or some other stimulus may reactivate the multiplication cycle, as shown in Figure 21.16.

Latency is part of the multiplication cycles of many kinds of viruses, not just bacteriophages. One case in point is Type I *Herpes simplex*, the cause of *cold sores* (fever blisters). Almost all humans harbor this virus. It remains latent in our facial tissues inside a ganglion. (A ganglion is a cluster of nerve cell bodies that each have one or more long, thin extensions called axons projecting from them.) Sunburn and other stress factors can reactivate the virus. When this happens, the virus particles move down to the axon endings and arrive near the surface of skin. There they infect epithelial cells and cause painful skin eruptions.

REVERSE TRANSCRIPTION OF VIRAL RNA

The multiplication cycle of RNA viruses has a twist to it. Inside a host cell's cytoplasm, their RNA functions as a template for synthesizing either DNA or mRNA. For example, HIV, a retrovirus, carts its own enzymes into cells. These assemble a DNA strand on viral RNA by reverse transcription (Sections 16.1 and 39.10).

Like other enveloped viruses, herpes viruses enter a host cell by their own version of endocytosis. Then new particles bud from the plasma membrane. Figure 21.16 shows how they accomplish this.

Viral multiplication cycles include five steps: Attachment to a suitable host cell, cell penetration, viral DNA or RNA replication and synthesis of viral proteins, assembly of new viral particles, and release from the infected cell.

Some bacteriophage replication cycles follow a rapid, lytic pathway and an extended, lysogenic pathway.

The replication cycles of RNA viruses involve the use of viral RNA as a template for synthesizing DNA or mRNA.

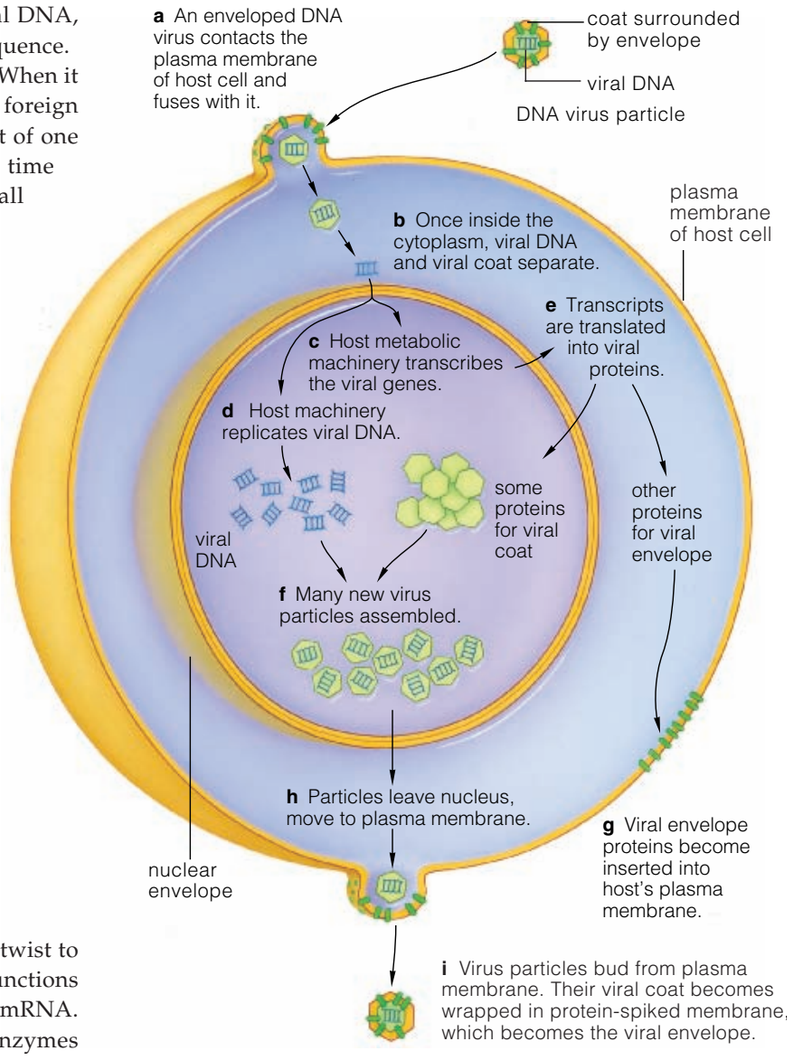


Figure 21.16 ***Animated!*** Multiplication cycle of one type of enveloped DNA virus, here infecting a generalized animal cell. Notice how part of the plasma membrane surrounds the budding viral particle. This is how some viruses get their envelope.

21.8 Evolution and Infectious Diseases

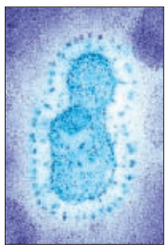
LINKS TO SECTIONS 17.3, 18.4

Just by being human, you are a targeted host for a staggering variety of pathogenic bacteria, viruses, fungi, protozoans, and parasitic worms.

The Nature of Disease "Disease" is something that just about everybody knows about but often has trouble explaining. Start with a few basic definitions. When a pathogen breaches the body's surface barriers and enters the internal environment, it may multiply inside cells or tissues. This is what **infection** means. **Disease** follows when the body's defenses cannot be mobilized quickly enough to keep a pathogen's activities from interfering with normal body functions. With *contagious* diseases, mucus, blood, or some other body fluid that harbors the pathogen must directly contact a new host.

Mycobacterium tuberculosis

In an *epidemic*, a disease spreads fast through part of a population in a limited time span, then subsides. In a *pandemic*, a disease breaks out in several countries at the same time. AIDS is pandemic. Sporadic diseases, such as whooping cough, occur irregularly and affect few people. Endemic diseases pop up more or less continually but do not spread far in large populations. Tuberculosis is like this. So is impetigo, a highly contagious bacterial infection that typically spreads no further than, say, a single day-care center.



SARS virus

AIDS is a pandemic that has no end in sight. A recent outbreak of *SARS* (severe acute respiratory syndrome) was a brief pandemic. It started in China, and travelers quickly carried it to countries around the world. Before government-ordered quarantines arrested its spread, thousands were sickened and hundreds died. A previously unknown coronavirus causes SARS. It has reappeared in China and may not subside completely.

An Evolutionary Perspective Consider disease in terms of a pathogen's prospects for survival. A pathogen stays around only for as long as it has access to outside sources of energy and raw materials. To a microscopic organism or virus, a human is a treasurehouse of both. With bountiful resources, a pathogen can multiply or replicate itself to amazing population sizes. Evolutionarily speaking, the ones that leave the most descendants win.

Two barriers prevent pathogens from evolving to a position of world dominance. First, any species that has a history of being attacked by a specific pathogen has coevolved with it and has built-in defenses against it, as by the vertebrate immune system. Second, if a pathogen kills too suddenly, it might disappear along with the individual host. This is one reason why most pathogens have less-than-fatal effects. After all, infected individuals who live longer spread more germs and contribute to a pathogen's reproductive or replicative success.

Usually, an individual dies only when it becomes host to overwhelming numbers of a pathogen, when it is a novel host with no coevolved defenses, or when a mutant pathogenic strain has emerged and has breached the current defenses.

Being equipped with an evolutionary perspective, you probably can perceive the connection on your own. The greater the population density of host individuals, the more kinds and greater frequencies of infectious diseases transmitted among them. This brings us to the bad news.

Emerging Pathogens Thanks to planes, trains, and automobiles, people travel often and in droves around the world. Among their exotic destinations are virgin tropical forests and other remote regions where the human body had been an infrequent or nonexistent opportunity for pathogens. Strange and often dangerous pathogens are opportunistic about the two-legged packages of nutrients entering their habitats. Within just a few hours, they may infect travelers, who often carry pathogens back home.

Some of these emerging pathogens have been around for a long time and are only now taking advantage of the presence of novel human hosts. Others are newly mutated strains of existing pathogens.

Ebola virus

Consider *Ebola*, one of several viruses that cause a dangerous hemorrhagic fever. It might have coevolved with monkeys in the tropical forests of Africa. By 1976, it was infecting humans. It kills between 70 and 90 percent of the people it infects. No vaccine or treatment is available for the disease, which starts with high fever and flu-like aches. Within a few days, nausea, vomiting, and diarrhea begin. Blood vessels are destroyed. Blood seeps from the circulatory system into the surrounding tissues and out through all the body's orifices. The liver and kidneys may rapidly turn to mush. Patients often become deranged and then die of

Table 21.3 The Eight Deadliest Infectious Diseases

Disease	Main Agents	Estimated New Cases per Year	Estimated Deaths per Year
Acute respiratory infections*	Bacteria, viruses	1 billion	4.7 million
Diarrheas**	Bacteria, viruses, protozoans	1.8 billion	3.1 million
Tuberculosis	Bacteria	9 million	3.1 million
Malaria	Sporozoans	110 million	2.5–2.7 million
AIDS	Virus (HIV)	5.6 million	2.6 million
Measles	Viruses	200 million	1 million
Hepatitis B	Virus	200 million	1 million
Tetanus	Bacteria	1 million	500,000

* Includes pneumonia, influenza, and whooping cough.
** Includes amoebic dysentery, cryptosporidiosis, and gastroenteritis.

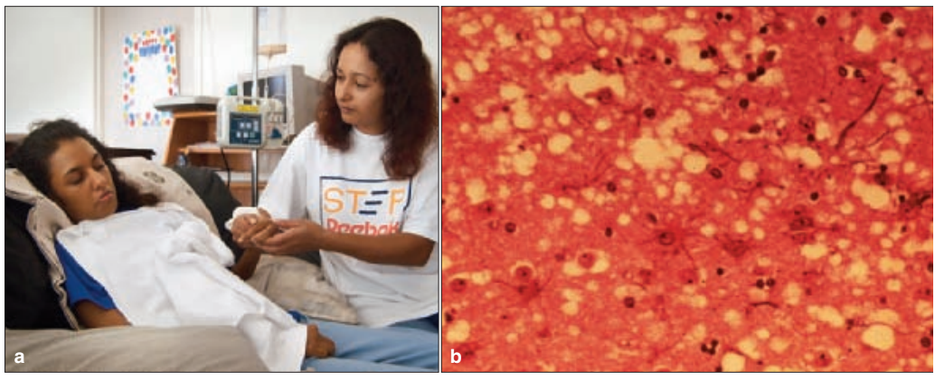
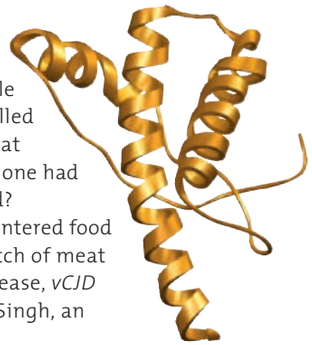


Figure 21.17 (**a**) Charlene Singh, the first known vCJD case in the United States, being cared for by her mother. She probably contracted the disease when she was growing up in Britain, before moving to Florida. Mood swings, balance problems, and memory loss started in 2001. She became confined to bed and could not control her body functions or communicate. She died in 2004.

(**b**) Section through a brain damaged by BSE. The light-colored "holes" are areas where tissue was destroyed. Below this micrograph is a model for a normal prion. The vCJD-causing version misfolds into a different three-dimensional structure.



circulatory shock. Understandably, at the start of an *Ebola* outbreak, government agencies throughout the world are mobilized. Quarantines can limit the pathogen's spread.

Drug-Resistant Strains There is an old saying that when you attack nature, it will come back at you with a pitchfork. Antibiotic resistance, explained in Section 18.4, has contributed to an upsurge in infectious diseases. For example, preschoolers have an immune system that is still developing. Increasing numbers are enrolled in day-care centers. *Streptococcus pneumoniae* and other pathogens slip through the crowded populations of hosts, causing pneumonia, meningitis, and chronic middle-ear infections. Each year, *S. pneumoniae* kills 40,000 to 50,000 people of all ages, even in hospitals. The drug-resistant strains are becoming the rule, not the exception.

Most of our 6.4 billion selves live in crowded cities. In any given interval, as many as 50 million of us are on the move within and between countries in search of a better life. Is it any wonder that agents of cholera, tuberculosis, and other diseases are spreading globally (Table 21.3)?

Foodborne Diseases and Mad Cows Each year, according to estimates from Centers for Disease Control, contaminated food sickens as many as 80 million people in the United States. The most vulnerable are the very young, the very old, or those with a weakened immune system. *Campylobacter*, *Salmonella*, *Staphylococcus aureus*, and *Listeria* are frequent contaminants of dairy products, meat, and poultry. All can cause abdominal pain, nausea, and diarrhea. *Listeria* infection during pregnancy may cause miscarriage or premature birth.

0157:H7 is one of the pathogenic strains of *E. coli*, a normally harmless bacterial species that inhabits your intestinal tract. Tons of ground beef contaminated with 0157:H7 have been recalled from vendors. Vegetarians also are at risk, because 0157:H7 has been found in fruit juices, lettuce, green onions, and alfalfa sprouts.

Bacteria are not the only foodborne threats. Consider *BSE* (bovine spongiform encephalopathy). The first case in the United States was reported in 2003. A single cow in Washington State developed this so-called *mad cow disease*. The government recalled meat from the herd and reassured consumers that none had entered the human food supply. What if it had?

Before 2000, thousands of cattle with BSE entered food chains, mainly in Great Britain. So far, that batch of meat has caused about 153 cases of a fatal brain disease, *vCJD* (variant Creutzfeldt–Jakob disease). Charlene Singh, an American, was one of the cases (Figure 21.17*a*).

A widely accepted hypothesis is that **prions** cause BSE, vCJD, and several other degenerative diseases in humans, cattle, and some wild animals, such as deer and elk.

Prions are certain protein particles that are present in normal tissues of the nervous system, where they are folded into a characteristic configuration (Figure 21.17*b*). Infectious prions are misfolded. In some unknown way, the altered protein shape induces the normal prions to become misfolded the same way.

Misfolded prions accumulate as massive deposits in the brain. Brain tissue samples taken from individuals who died from prion-induced diseases are riddled with holes. Collectively, the holes give brain tissue a spongelike (spongiform) appearance, as in Figure 21.17*b*.

The kinds of prions that cause BSE and vCJD are nearly identical. They might be mutated strains of the prions that cause *scrapie*, a degenerative disease in sheep. Some prions apparently were transferred from sheep to cattle by way of livestock feed that contained animal parts. Governments banned the use of such feed.

Prions are not alive, so they cannot be killed. It is not easy to destroy them by denaturation methods of boiling, baking, irradiation, and application of most disinfectants.

Should you worry about eating American beef? The USDA says no. If you are a beef lover and a skeptic, you might wish to avoid eating brains or meat cuts that contain spinal cord, such as oxtails. Ground beef and sausage may accidentally contain nervous tissue, so watch how it is being made or make your own. You may also want to look for meat from grass-fed cattle.

Summary

Section 21.1 Bacteria and archaeans are prokaryotic cells; they do not have a nucleus. Some have membrane infoldings and other structures in the cytoplasm. None has a profusion of organelles.

Three cell shapes are common: cocci (spheres), bacilli (rods), and spirilla (spirals). Nearly all bacteria have a cell wall with peptidoglycans that protects the plasma membrane and resists rupturing. Often a sticky mesh of polysaccharides (a glycocalyx) surrounds the wall as a capsule or slime layer. Some species have one or more bacterial flagella, or motile structures that rotate like a propeller. Many have pili: filamentous proteins that help cells adhere to a surface or that facilitate conjugation.

Collectively, prokaryotes show metabolic diversity, as in modes of acquiring energy and carbon. Cyanobacteria and other *photoautotrophs* use sunlight and carbon dioxide during photosynthesis. Some bacteria and archaeans are *photoheterotrophs*; they use sunlight energy but get carbon from organic compounds. *Chemoautotrophs*, such as the nitrifying bacteria, use carbon dioxide but make ATP by stripping electrons from organic or inorganic substances. Most prokaryotes are *chemoheterotrophs* that range from decomposers, pathogens, and parasites to saprobes.

Biology Now

Explore prokaryotic structure with the animation on BiologyNow.

Section 21.2 Only bacteria and archaeans divide by prokaryotic fission: replication of a single, circular bacterial chromosome and division of a parent cell into two genetically equivalent daughter cells. Many species have plasmids: small circles of DNA that are replicated independently. They can transfers plasmids to cells of the same or different species by bacterial conjugation.

Biology Now

Observe prokaryotic fission and conjugation with the animation on BiologyNow.

Section 21.3 Traditionally, any newly discovered prokaryote was classified by the total number of traits it shares with a known prokaryotic group. Biochemical comparisons are clarifying phylogenies. Groups are being assigned to domains Bacteria and Archaea.

Section 21.4 Bacteria are the most ancient lineages of prokaryotic cells, and they are metabolically diverse. Most are chemoheterotrophs, and many of these species are parasites and pathogens.

Some major groups are cyanobacteria, proteobacteria, chlamydia, spirochaetes, and Gram-positive bacteria. The proteobacteria are the most diverse monophyletic group.

Section 21.5 Archaeans are prokaryotic. They are like bacteria in size, shape, not having a nucleus, having operons, and other respects. They are unique in other respects, as in their cell wall composition. Archaeans also resemble eukaryotes—for example, in some aspects of gene transcription and translation. They are now classified in their own domain, separate from bacteria. These prokaryotes show far greater distribution and diversity than was previously suspected.

Comparative rRNA studies give evidence of three archaean groups: euryarchaeotes, crenarchaeotes, and korarchaeotes. Most archaean methanogens (methane makers) and halophiles (salt lovers) belong to the first group, and most of the archaean extreme thermophiles belong to the second group.

Archaeans and bacteria coexist in many hospitable as well as hostile habitats, and apparently they engage in gene transfers.

Section 21.6 All viruses are noncellular infectious particles that attack specific kinds of host species.

Each virus particle consists of a core of DNA or RNA and a protein coat that sometimes is enclosed in a lipid envelope. Many glycoproteins project like spikes from the envelopes. The coats of complex viruses also have sheaths, tail fibers, and other accessory structures.

A virus particle multiplies only after its genetic material enters a host cell and directs synthesis of the molecules necessary to produce new virus particles.

Biology Now

Compare viral forms with the animation on BiologyNow.

Section 21.7 Nearly all viral multiplication cycles have five steps: attachment to a suitable host cell, cell penetration, viral DNA or RNA replication followed by protein synthesis, assembly of new viral particles, and release. Two pathways are common in multiplication cycles of bacteriophages (bacteria-infecting viruses).

In a lytic pathway, multiplication is fast; new viral particles are released by lysis.

In a lysogenic pathway, the infection enters a latent period. A host cell is not killed outright, and the viral nucleic acid may undergo recombination with a host cell chromosome.

Multiplication cycles of viruses are diverse. Besides varying in their duration, the penetration and release of most enveloped types occur by endocytosis and budding. DNA viruses spend part of the cycle in the nucleus of a host cell. RNA viruses complete the replication cycle in the cytoplasm. The viral RNA is the template for mRNA synthesis and for protein synthesis.

Biology Now

Learn how viruses can multiply with the animation on BiologyNow.

Section 21.8 Infection is the invasion of a cell or multicelled body by a pathogen, which causes disease when its activities interfere with body functions. Hosts and pathogens coevolve. Antibiotics and antiviral drugs select for drug-resistant strains. Many bacteria cause food poisoning. Prions are infectious proteins that kill by destroying the brain and nervous tissue.

Biology Now

Read the InfoTrac article "Origins of HIV: The Interrelationship Between Nonhuman Primates and the Virus," Myrna Watanabe, Bioscience, *September 2004.*

Self-Quiz

Answers in Appendix II

1. Only _____ are prokaryotic.
   a. archaeans c. prions
   b. bacteria d. both a and b

2. Bacteria transfer plasmids by _____ .
   a. prokaryotic fission c. conjugation
   b. endospore formation d. the lytic pathway

3. The _____ are all oxygen-releasing photoautotrophs.
   a. spirochetes c. cyanobacteria
   b. chlamydias d. proteobacteria

4. The normally harmless *E. coli* in your gut are _____ .
   a. spirochetes c. cyanobacteria
   b. chlamydias d. proteobacteria

5. All _____ are intracellular parasites of vertebrates.
   a. spirochetes c. cyanobacteria
   b. chlamydias d. proteobacteria

6. Some Gram-positive bacteria (e.g., *Bacillus anthracis*) survive harsh conditions by forming a(n) _____ .
   a. pilus c. endospore
   b. heterocyst d. plasmid

7. Only _____ reproduce by prokaryotic fission.
   a. viruses c. bacteria
   b. archaeans d. b and c are correct

8. DNA or RNA may be the genetic material of _____ .
   a. bacteria b. a virus c. archaeans d. a prion

9. Is this statement false: All known viruses consist of genetic material, a protein coat, and an outer envelope.

10. Bacteriophages can multiply by _____ .
    a. prokaryotic fission c. the lysogenic pathway
    b. the lytic pathway d. both b and c

11. Match the terms with their most suitable description.
    ____ archaean a. infectious protein
    ____ bacteria b. nonliving infectious particle; nucleic acid core, protein coat
    ____ virus
    ____ plasmid c. prelude to conjugation
    ____ extreme halophile d. prokaryotes that most closely resemble eukaryotes
    ____ prion e. most common prokaryotic cells
    ____ sex pilus f. small circle of bacterial DNA
    g. salt lover

Additional questions are available on Biology Now™

Critical Thinking

1. Annual costs of treating known cases of food poisoning are between 5 billion and 22 billion dollars, and pathogens in kitchens may cause at least half of the cases. Electron microscopes show microbes on wood or plastic cutting boards, even stainless steel knives (Figure 21.18). Carlos Enriquez and his colleagues at the University of Arizona sampled 75 dishrags and 325 sponges in some homes. They found *Salmonella*, *E. coli*, *Pseudomonas*, and *Staphylococcus* colonies in most of them. Bacteria can live for as long as two weeks in a wet sponge (which can be sanitized in one dishwasher cycle). If your class has access to a good light microscope, each of you bag one of your kitchen sponges or dishrags and compare what might be living with you.

Figure 21.18 On a kitchen knife's blade, bits of food and *Pseudomonas*. The cell's pili attached to the blade. Think about it next time you use any unwashed kitchen utensil that contacted raw beef, poultry, or seafood.

2. One way to prevent bacterial food poisoning is by *food irradiation*, exposing food to high-energy rays or beams that kill pathogenic bacteria. The process also slows spoilage and prolongs shelf life. Some think this is a safe way to protect consumers. Others think the treatment could produce harmful chemicals. They say irradiation does not kill endospores that can cause botulism. In their view, the best way to prevent food poisoning is to tighten and enforce food safety standards.

   Irradiated meat, poultry, and fruits are now available in many supermarkets. By law, they must be marked with the symbol shown at right. Would seeing this symbol on a package make you more or less likely to purchase the product? Explain your answer.

3. *Thermotoga maritima* was discovered in geothermically heated marine sediments and prefers water of about 80°C. Analysis of rRNA puts it in the bacterial group, but gene sequencing of the entire genome reveals a more complex picture. About 50 percent of *T. maritima* genes resemble bacterial genes, about 25 percent of its genes are unique, and about 25 percent resemble those of archaeans, the thermophile *Pyrococcus horikoshii* in particular. Suggest two possible explanations for the similarity between these prokaryotes of different domains.

4. Some picornavirus strains cause the highly contagious *foot and mouth disease*. Hosts include cattle, water buffalo, sheep, and pigs. Symptoms include extensive lesions and major tissue erosion, lameness, weight loss, milk loss, and often death. The viral strain causing a recent epidemic was first identified in Asia, then in Europe and elsewhere. It devastated farmers still recovering from a BSE outbreak. There is no vaccine; at this writing, more than a million animals have been destroyed to stop the spread of the disease. Research the impact of this virus on travel and the global economy. Hint: Start at http://www.cdc.gov/.

5. Do you think that the whole world would be better off without viruses? If so, consider this: Curtis Suttle at the University of British Columbia studies interactions among viruses, bacteria, and algae in ocean water. He selectively removed viruses from seawater samples—and the algae in the water stopped growing. Suttle found that they were dependent on nutrients released by dying bacteria, which lyse after viral infection. Make a list of some other ways in which viruses might be integrated into ecosystems.