4

Cell Structure and Function in the *Bacteria* and *Archaea*

Our planet has always been in the "Age of Bacteria," ever since the first fossils—bacteria of course—were entombed in rocks more than 3 billion years ago. On any possible, reasonable criterion, bacteria are—and always have been—the dominant forms of life on Earth.
—Paleontologist Stephen J. Gould (1941–2002)

"Double, double toil and *trouble; Fire burn, and cauldron bubble*" is the refrain repeated several times by the chanting witches in Shakespeare's *Macbeth* (Act IV, Scene 1). This image of a hot, boiling cauldron actually describes the environment in which many bacterial, and especially archaeal, species happily grow! For example, some species can be isolated from hot springs or the hot, acidic mud pits of volcanic vents (FIGURE 4.1).

When the eminent evolutionary biologist and geologist Stephen J. Gould wrote the opening quote of this chapter, he as well as most microbiologists had no idea that embedded in these "bacteria" was another whole domain of organisms. Thanks to the pioneering studies of Carl Woese and his colleagues, it now is quite evident there are two distinctly different groups of "prokaryotes"—the *Bacteria* and the *Archaea* (see Chapter 3). Many of the organisms Woese and others studied are organisms that would live a happy life in a witch's cauldron because they can grow at high temperatures, produce methane gas, or survive in extremely acidic and hot environments—a real cauldron! Termed **extremophiles**, these members of the domains *Bacteria*

Chapter Preview and Key Concepts

4.1 Diversity among the *Bacteria* and *Archaea*
1. The *Bacteria* are classified into several major phyla.
2. The *Archaea* are currently classified into two major phyla.

4.2 Cell Shapes and Arrangements
3. Many bacterial cells have a rod, spherical, or spiral shape and are organized into a specific cellular arrangement.

4.3 An Overview to Bacterial and Archaeal Cell Structure
4. Bacterial and archaeal cells are organized at the cellular and molecular levels.

4.4 External Cell Structures
5. Pili allow cells to attach to surfaces or other cells.
6. Flagella provide motility.
7. A glycocalyx protects against desiccation, attaches cells to surfaces, and helps pathogens evade the immune system.

4.5 The Cell Envelope
8. Bacterial cell walls help maintain cell shape and protect the cell membrane from rupture.
9. Archaeal cell walls have crystalline layers.
10. Molecules and ions cross the cell membrane by facilitated diffusion or active transport.
11. Archaeal membranes are structurally unique.

4.6 The Cell Cytoplasm and Internal Structures
12. The nucleoid contains the cell's essential genetic information.
13. Plasmids contain nonessential genetic information.
14. Ribosomes, microcompartments, and inclusions carry out specific intracellular functions.
15. Cytoskeletal proteins regulate cell division and help determine cell shape.

4.7 The Bacteria/Eukaryote Paradigm—Revisited
16. Cellular processes in bacterial cells can be similar to those in eukaryatic cells.
MICROINQUIRY 4: The Prokaryote/Eukaryote Model

(A) (B)

FIGURE 4.1 Life at the Edge. Bacterial and archaeal extremophiles have been isolated from the edges of natural cauldrons, including (**A**) the Grand Prismatic Spring in Yellowstone National Park, Wyoming, where the water of the hot spring is over 70°C, or (**B**) the mud pools surrounding sulfurous steam vents of the Solfatara Crater in Pozzuoli, Italy, where the mud has a very low pH and a temperature above 90°. »» How do extremophiles survive under these extreme conditions?

and *Archaea* have a unique genetic makeup and have adapted to extreme environmental conditions.

In fact, Gould's "first fossils" may have been archaeal species. Many microbiologists believe the ancestors of today's archaeal species might represent a type of organism that first inhabited planet Earth when it was a young, hot place (see MicroFocus 2.1). These unique characteristics led Woese to propose these organisms be lumped together and called the Archaebacteria (*archae* = "ancient").

Since then, the domain name has been changed to *Archaea* because (1) not all members are extremophiles or related to these possible ancient ancestors and (2) they are not *Bacteria*—they are *Archaea*. Some might also debate using the term prokaryotes when referring to both domains, as organisms in the two domains are as different from each other as they are from the *Eukarya*.

As more microbes have had their complete genomes sequenced, it now is clear that there are unique as well as shared characteristics between species in the domains *Bacteria* and *Archaea*.

In this chapter, we examine briefly some of the organisms in the domains *Bacteria* and *Archaea*. However, because almost all known "prokaryotic" pathogens of humans are in the domain *Bacteria*, we emphasize structure within this domain. As we see in this chapter, a study of the structural features of bacterial cells provides a window to their activities and illustrates how the *Bacteria* relate to other living organisms.

As we examine bacterial and archaeal cell structure, we can assess the dogmatic statement that these cells are characterized by a lack of a cell nucleus and internal membrane-bound organelles. Before you finish this chapter, you will be equipped to revise this view.

4.1 Diversity among the *Bacteria* and *Archaea*

In this section, we discuss bacterial and archaeal diversity using the current classification scheme, which is based in large part on nucleotide sequence data. There are some 7,000 known bacterial and archaeal species and a suspected 10 million species. In this section, we will highlight a few phyla and groups using the phylogenetic tree in FIGURE 4.2.

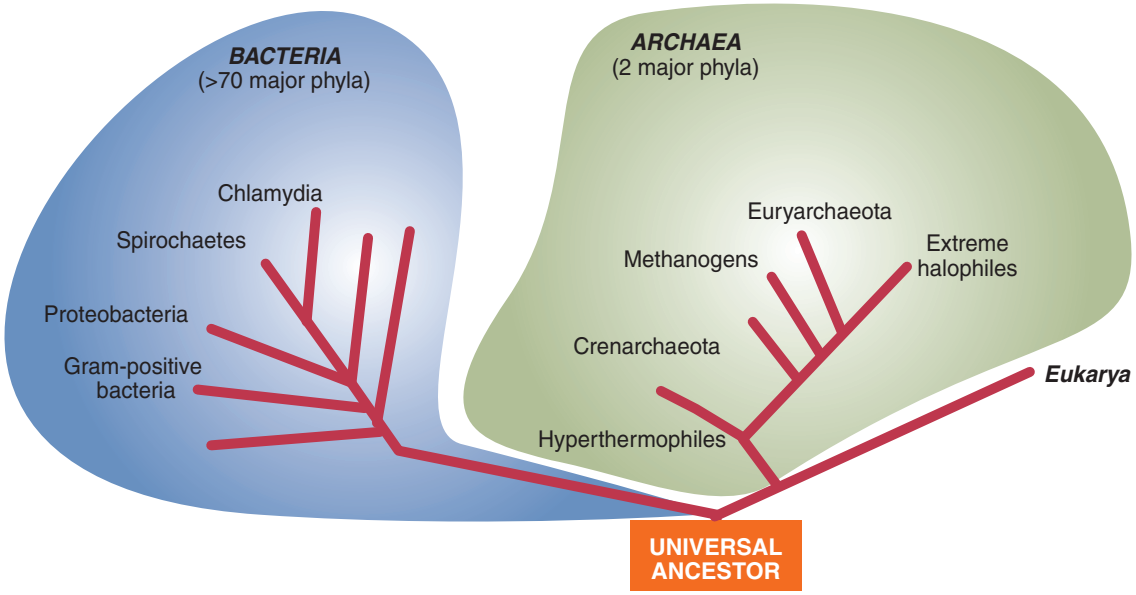


FIGURE 4.2 The Phylogenetic Tree of *Bacteria* and *Archaea*. The tree shows several of the bacterial and archaeal phyla discussed in this chapter. »» What is common to the branch base of both the *Bacteria* and *Archaea*?

The Domain *Bacteria* Contains Some of the Most Studied Microbial Organisms

KEY CONCEPT

1. The *Bacteria* are classified into several major phyla.

There are about 18 phyla of *Bacteria* identified from culturing or nucleotide sequencing. It should come as no shock to you by now to read that the vast majority of these phyla play a positive role in nature (MicroFocus 4.1). Although not unique to just the bacterial phyla, they digest sewage into simple chemicals; they extract nitrogen from the air and make it available to plants for protein production; they break down the remains of all that die and recycle the carbon and other elements; and they produce oxygen gas that we and other animals breathe.

Of course, we know from Chapter 1 and personal experience that some bacterial organisms are harmful—many human pathogens are members of the domain *Bacteria*. Certain species multiply within the human body, where they disrupt tissues or produce toxins that result in disease.

The *Bacteria* have adapted to the diverse environments on Earth, inhabiting the air, soil, and water, and they exist in enormous numbers on the surfaces of virtually all plants and animals. They can be isolated from Arctic ice, thermal hot springs, the fringes of space, and the tissues of animals. Bacterial species, along with their archaeal relatives, have so completely colonized every part of the Earth that their mass is estimated to outweigh the mass of all plants and animals combined. Let's look briefly at some of the major phyla and other groups.

Proteobacteria. The **Proteobacteria** (*proteo* = "first") contains the largest and most diverse group of species and includes many familiar gram-negative genera, such as *Escherichia* (FIGURE 4.3A). The phylum also includes some of the most recognized human pathogens, including species of *Shigella, Salmonella, Neisseria* (responsible for gonorrhea), *Yersinia* (responsible for plague), and *Vibrio* (responsible for cholera). It is likely that the mitochondria of the *Eukarya* were derived through endosymbiosis from an ancestor of the Proteobacteria (see MicroInquiry 3).

The group also includes the rickettsiae (sing., rickettsia), which were first described by Howard Taylor Ricketts in 1909. These tiny bacterial cells can barely be seen with the most powerful light microscope. They are transmitted among humans primarily by arthropods, and are cultivated only in living tissues such as chick embryos. Different species cause a number of important diseases, including Rocky Mountain spotted fever and

Arthropods: Animals having jointed appendages and segmented body (e.g., ticks, lice, fleas, mosquitoes).

MICROFOCUS 4.1

Bacteria in Eight Easy Lessons[1]

Mélanie Hamon, an assistante de recherché at the Institut Pasteur in Paris, says that when she introduces herself as a bacteriologist, she often is asked, "Just what does that mean?" To help explain her discipline, she gives us, in eight letters, what she calls "some demystifying facts about bacteria."

Basic principles: Their average size is 1/25,000th of an inch. In other words, hundreds of thousands of bacteria fit into the period at the end of this sentence. In comparison, human cells are 10 to 100 times larger with a more complex inner structure. While human cells have copious amounts of membrane-contained subcompartments, bacteria more closely resemble pocketless sacs. Despite their simplicity, they are self-contained living beings, unlike viruses, which depend on a host cell to carry out their life cycle.

Astonishing: Bacteria are the root of the evolutionary tree of life, the source of all living organisms. Quite successful evolutionarily speaking, they are ubiquitously distributed in soil, water, and extreme environments such as ice, acidic hot springs or radioactive waste. In the human body, bacteria account for 10% of dry weight, populating mucosal surfaces of the oral cavity, gastrointestinal tract, urogenital tract and surface of the skin. In fact, bacteria are so numerous on earth that scientists estimate their biomass to far surpass that of the rest of all life combined.

Crucial: It is a little known fact that most bacteria in our bodies are harmless and even essential for our survival. Inoffensive skin settlers form a protective barrier against any troublesome invader while approximately 1,000 species of gut colonizers work for our benefit, synthesizing vitamins, breaking down complex nutrients and contributing to gut immunity. Unfortunately for babies (and parents!), we are born with a sterile gut and "colic" our way through bacterial colonization.

Tools: Besides the profitable relationship they maintain with us, bacteria have many other practical and exploitable properties, most notably, perhaps, in the production of cream, yogurt and cheese. Less widely known are their industrial applications as antibiotic factories, insecticides, sewage processors, oil spill degraders, and so forth.

Evil: Unfortunately, not all bacteria are "good," and those that cause disease give them all an often undeserved and unpleasant reputation. If we consider the multitude of mechanisms these "bad" bacteria—pathogens—use to assail their host, it is no wonder that they get a lot of bad press. Indeed, millions of years of coevolution have shaped bacteria into organisms that "know" and "predict" their hosts' responses. Therefore, not only do bacterial toxins know their target, which is never missed, but bacteria can predict their host's immune response and often avoid it.

Resistant: Even more worrisome than their effectiveness at targeting their host is their faculty to withstand antibiotic therapy. For close to 50 years, antibiotics have revolutionized public health in their ability to treat bacterial infections. Unfortunately, overuse and misuse of antibiotics have led to the alarming fact of resistance, which promises to be disastrous for the treatment of such diseases.

Ingenious: The appearance of antibiotic-resistant bacteria is a reflection of how adaptable they are. Thanks to their large populations they are able to mutate their genetic makeup, or even exchange it, to find the appropriate combination that will provide them with resistance. Additionally, bacteria are able to form "biofilms," which are cellular aggregates covered in slime that allow them to tolerate antimicrobial applications that normally eradicate free-floating individual cells.

A long tradition: Although "little animalcules" were first observed in the 17th century, it was not until the 1850s that Louis Pasteur fathered modern microbiology. From this point forward, research on bacteria has developed into the flourishing field it is today. For many years to come, researchers will continue to delve into this intricate world, trying to understand how the good ones can help and how to protect ourselves from the bad ones. It is a great honor to be part of this tradition, working in the very place where it was born.

[1]Republished with permission of the author, the Institut Pasteur, and the Pasteur Foundation. The original article appeared in *Pasteur Perspectives* Issue 20 (Spring 2007), the newsletter of the Pasteur Foundation, which may be found at www.pasteurfoundation.org © Pasteur Foundation.

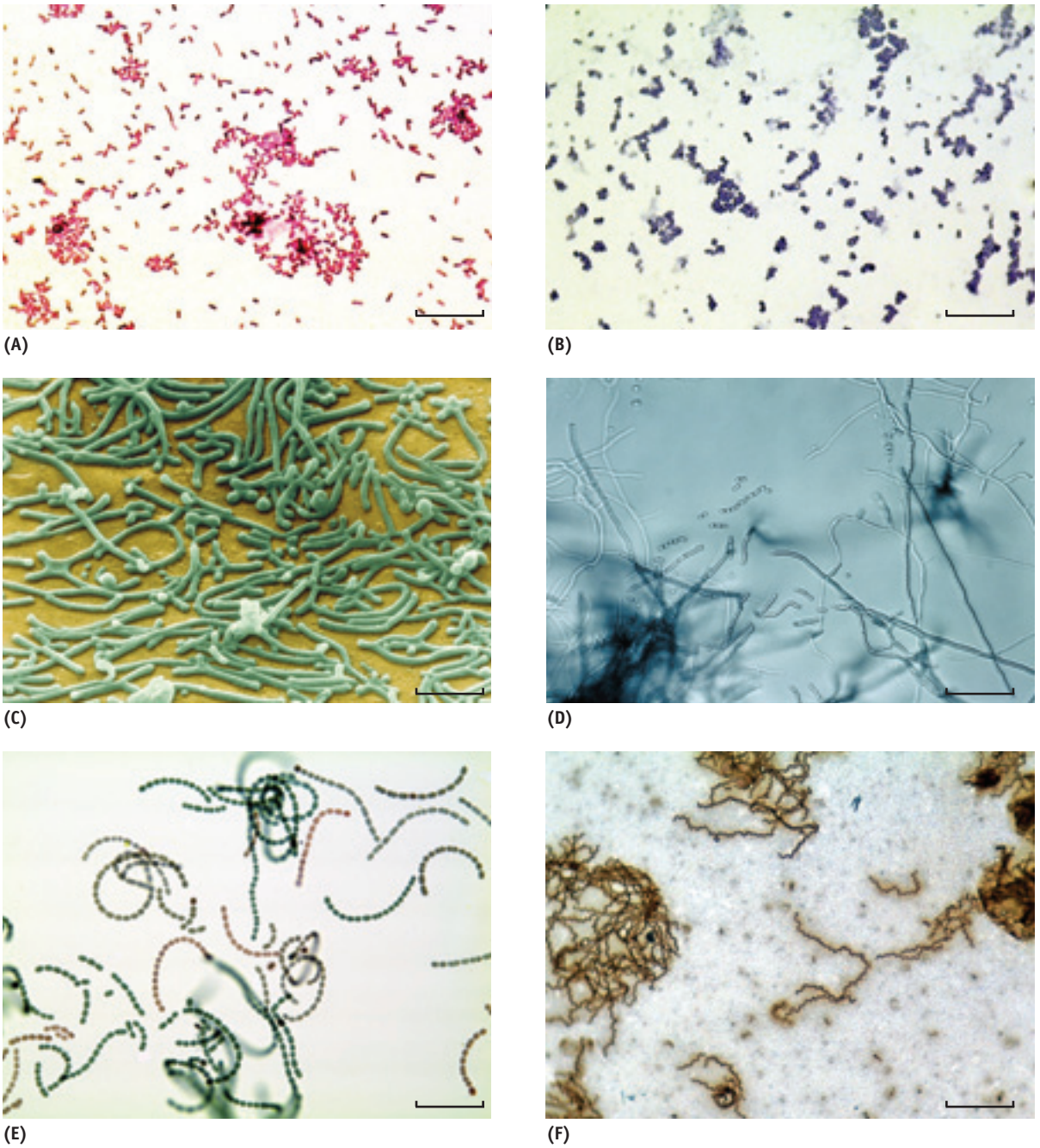


FIGURE 4.3 Members of the Domain *Bacteria*. (**A**) *Escherichia coli* (Bar = 10 µm.), (**B**) *Staphylococcus aureus* (Bar = 10 µm.), (**C**) *Mycoplasma* species (Bar = 2 µm.), (**D**) *Streptomyces* species (Bar = 20 µm.), (**E**) *Anabaena* species (Bar = 100 µm.), and (**F**) *Treponema pallidum* (Bar = 10 µm.). All images are light micrographs except (**C**), a false-color scanning electron micrograph. »» What is the Gram staining result for *E. coli* and *S. aureus*?

typhus fever. Chapter 12 contains a more thorough description of their properties.

Firmicutes. The **Firmicutes** (*firm* = "strong"; *cuti* = "skin") consists of many species that are gram-positive. As we will see in this chapter, they share a similar thick "skin," which refers to their cell wall structure. Genera include *Bacillus* and *Clostridium*, specific species that are responsible for anthrax and botulism, respectively. Species within the genera *Staphylococcus* and *Streptococcus* are responsible for several mild to life-threatening human illnesses (FIGURE 4.3B).

Also within the Firmicutes is the genus *Mycoplasma*, which lacks a cell wall but is otherwise

phylogenetically related to the gram-positive bacterial species (FIGURE 4.3C). Possibly the smallest free-living bacterial cell, one species causes a form of pneumonia (Chapter 10) while another mycoplasmal illness represents a sexually-transmitted disease (Chapter 13).

Actinobacteria. Another phylum of gram-positive species is the **Actinobacteria**. Often called the actinomycetes, these bacterial organisms form a system of branched filaments that somewhat resemble the growth form of fungi. The genus *Streptomyces* is the source for important antibiotics (FIGURE 4.3D). Another medically important genus is *Mycobacterium,* one species of which is responsible for tuberculosis.

Cyanobacteria. In Chapter 3 we discussed the cyanobacteria. They are phylogenetically related to the gram-positive species and can exist as unicellular, filamentous, or colonial forms (FIGURE 4.3E). Once known as blue-green algae because of their pigmentation, pigments also may be black, yellow, green, or red. The periodic redness of the Red Sea, for example, is due to blooms of cyanobacteria whose members contain large amounts of red pigment.

Blooms: Sudden increases in the numbers of cells of an organism in an environment.

The phylum **Cyanobacteria** are unique among bacterial groups because they carry out photosynthesis similar to unicellular algae (Chapter 6) using the light-trapping pigment chlorophyll. Their evolution on Earth was responsible for the "oxygen revolution" that transformed life on the young planet. In addition, chloroplasts probably are derived from the endosymbiotic union with a cyanobacterial ancestor.

Chlamydiae. Roughly half the size of the rickettsiae, members of the phylum **Chlamydiae** are so small that they cannot be seen with the light microscope and are cultivated only within living cells. Most species in the phylum are pathogens and one species causes the gonorrhea-like disease known as chlamydia. Chlamydial diseases are described in Chapter 13.

Spirochaetes. The phylum **Spirochaetes** contains more than 340 gram-negative species that possess a unique cell body that coils into a long helix and moves in a corkscrew pattern. The ecological niches for the spirochetes is diverse: from free-living species found in mud and sediments, to symbiotic species present in the digestive tracts of insects, to the pathogens found in the urogenital tracts of vertebrates. Many spirochetes are found in the human oral cavity; in fact, some of the first animalcules seen by Leeuwenhoek were probably spirochetes from his teeth scrapings (see Chapter 1). Among the human pathogens are *Treponema pallidum*, the causative agent of syphilis and one of the most common sexually transmitted diseases (FIGURE 4.3F; Chapter 13); and specific species of *Borrelia*, which are transmitted by ticks or lice and are responsible for Lyme disease and relapsing fever (Chapter 12).

Other Phyla. There are many other phyla within the domain *Bacteria*. Several lineages branch off near the root of the domain. The common link between these organisms is that they are **hyperthermophiles**; they grow at high temperatures. Examples include *Aquifex* and *Thermotoga,* which typically are found in earthly cauldrons such as hot springs.

CONCEPT AND REASONING CHECKS

4.1 What three unique events occurred within the Proteobacteria and Cyanobacteria that contributed to the evolution of the Eukarya and the oxygen-rich atmosphere on Earth?

The Domain *Archaea* Contains Many Extremophiles

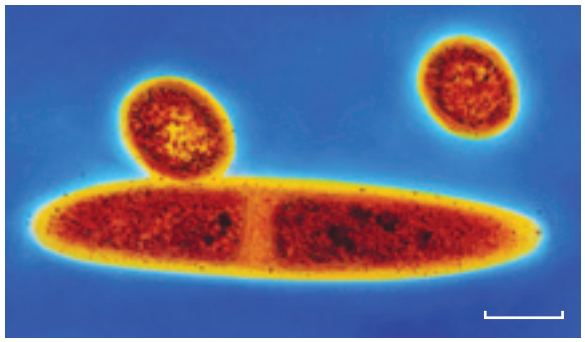
KEY CONCEPT

2. The *Archaea* are currently classified into two major phyla.

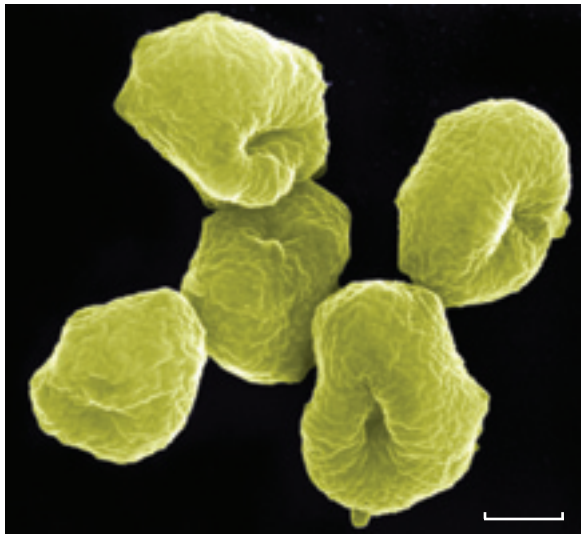
Classification within the domain *Archaea* has been more difficult than within the domain *Bacteria,* in large part because they have not been studied as long as their bacterial counterparts.

Archaeal organisms are found throughout the biosphere. Many genera are extremophiles, growing best at environmental extremes, such as very high temperatures, high salt concentrations, or extremes of pH. However, most species exist in very cold environments although there are archaeal genera that thrive under more modest conditions. The archaeal genera can be placed into one of two major phyla.

Euryarchaeota. The **Euryarchaeota** contain organisms with varying physiologies, many being extremophiles. Some groups, such as the **methanogens** (*methano* = "methane"; *gen* = "produce") are killed by oxygen gas and therefore are found in environments devoid of oxygen gas. The pro-



(A)



(C)

(B)

FIGURE 4.4 Members of the Domain *Archaea*. (**A**) A false-color transmission electron micrograph of the methanogen *Methanospirillum hungatei*. (Bar = 0.5 µm.) (**B**) An aerial view above Redwood City, California, of the salt ponds whose color is due to high concentrations of extreme halophiles. (**C**) A false-color scanning electron micrograph of *Sulfolobus*, a hyperthermophile that grows in waters as hot as 90°C. (Bar = 0.5 µm.) »» What advantage is afforded these species that grow in such extreme environments?

duction of methane (natural) gas is important in their energy metabolism (FIGURE 4.4A). In fact, these archaeal species release more than 2 billion tons of methane gas into the atmosphere every year. About a third comes from the archaeal species living in the stomach (rumen) of cows (see Chapter 2).

Another group is the **extreme halophiles** (*halo* = "salt"; *phil* = "loving"). They are distinct from the methanogens in that they require oxygen gas for energy metabolism and need high concentrations of salt (NaCl) to grow and reproduce. The fact that they often contain pink pigments makes their identification easy (FIGURE 4.4B). In addition, some extreme halophiles have been found in lakes where the pH is greater than 11.

A third group is the **hyperthermophiles** that grow optimally at high temperatures approaching or surpassing 100°C.

Crenarchaeota. The second phylum, the **Crenarchaeota**, are mostly hyperthermophiles growing at temperatures above 80°C. Hot sulfur springs are one environment where these archaeal species also thrive. The temperature is around 75°C but the springs are extremely acidic (pH of 2–3). Volcanic vents are another place where these organisms can survive quite happily (FIGURE 4.4C). Other species are dispersed in open oceans, often inhabiting the cold ocean waters (–3°C) of the deep sea environments and polar seas.

TABLE 4.1 summarizes some of the characteristics that are shared or are unique among the three domains.

CONCEPT AND REASONING CHECKS

4.2 Compared to the more moderate environments in which some archaeal species grow, why have others adapted to such extreme environments?

TABLE

4.1 Some Major Differences between *Bacteria*, *Archaea*, and *Eukarya*

Characteristic	*Bacteria*	*Archaea*	*Eukarya*
Cell nucleus	No	No	Yes
Chromosome form	Single, circular	Single, circular	Multiple, linear
Histone proteins present	No	Yes	Yes
Peptidoglycan cell wall	Yes	No	No
Membrane lipids	Ester-linked	Ether-linked	Ester-linked
Ribosome sedimentation value	70S	70S	80S
Ribosome sensitivity to diphtheria toxin	No	Yes	Yes
First amino acid in a protein	Formylmethionine	Methionine	Methionine
Chlorophyll-based photosynthesis	Yes (cyanobacteria)	No	Yes (algae)
Growth above 80°C	Yes	Yes	No
Growth above 100°C	No	Yes	No

4.2 Cell Shapes and Arrangements

Bacterial and archaeal cells come in a bewildering assortment of sizes, shapes, and arrangements, reflecting the diverse environments in which they grow. As described in Chapter 3, these three characteristics can be studied by viewing stained cells with the light microscope. Such studies show that most, including the clinically significant ones, appear in one of three different shapes: the rod, the sphere, or the spiral.

Variations in Cell Shape and Cell Arrangement Exist

KEY CONCEPT

3. Many bacterial cells have a rod, spherical, or spiral shape and are organized into a specific cellular arrangement.

A bacterial cell with a rod shape is called a **bacillus** (pl., bacilli). In various species of rod-shaped bacteria, the cylindrical cell may be as long as 20 µm or as short as 0.5 µm. Certain bacilli are slender, such as those of *Salmonella typhi* that cause typhoid fever; others, such as the agent of anthrax *(Bacillus anthracis)*, are rectangular with squared ends; still others, such as the diphtheria bacilli *(Corynebacterium diphtheriae)*, are club shaped. Most rods occur singly, in pairs called **diplobacillus**, or arranged into a long chain called **streptobacillus** (*strepto* = "chains") (FIGURE 4.5A). Realize there are two ways to use the word "bacillus": to denote a rod-shaped bacterial cell, and as a genus name (*Bacillus*).

A spherically shaped bacterial cell is known as a **coccus** (pl., cocci; *kokkos* = "berry") and tends to be quite small, being only 0.5 µm to 1.0 µm in diameter. Although they are usually round, they also may be oval, elongated, or indented on one side. Many bacterial species that are cocci stay together after division and take on cellular arrangements characteristic of the species (FIGURE 4.5B). Cocci remaining in a pair after reproducing represent a **diplococcus**. The organism that causes gonorrhea, *Neisseria gonorrhoeae*, and one type of bacterial meningitis *(N. meningitidis)* are diplococci. Cocci that remain in a chain are called **streptococcus**. Certain species of streptococci are involved in strep throat *(Streptococcus pyogenes)* and tooth decay *(S. mutans)*, while other species are harmless enough to be used for producing dairy products such as yogurt *(S. lactis)*. Another arrangement of cocci is the **tetrad**, consisting of four cocci forming a square. A cube-like packet of eight cocci is called a **sarcina** (*sarcina* = "bundle"). *Micrococcus luteus*, a common inhabitant of the skin, is one example. Other cocci may divide randomly and form an irregular grape-like cluster of cells called a **staphylococcus** (*staphylo* = "cluster"). A well-known example, *Staphylococcus aureus*, is often a cause of food poisoning, toxic shock syndrome, and several skin infections. The latter are known in the modern vernacular as "staph" infections. Notice again that the words "streptococcus" and "staphy-

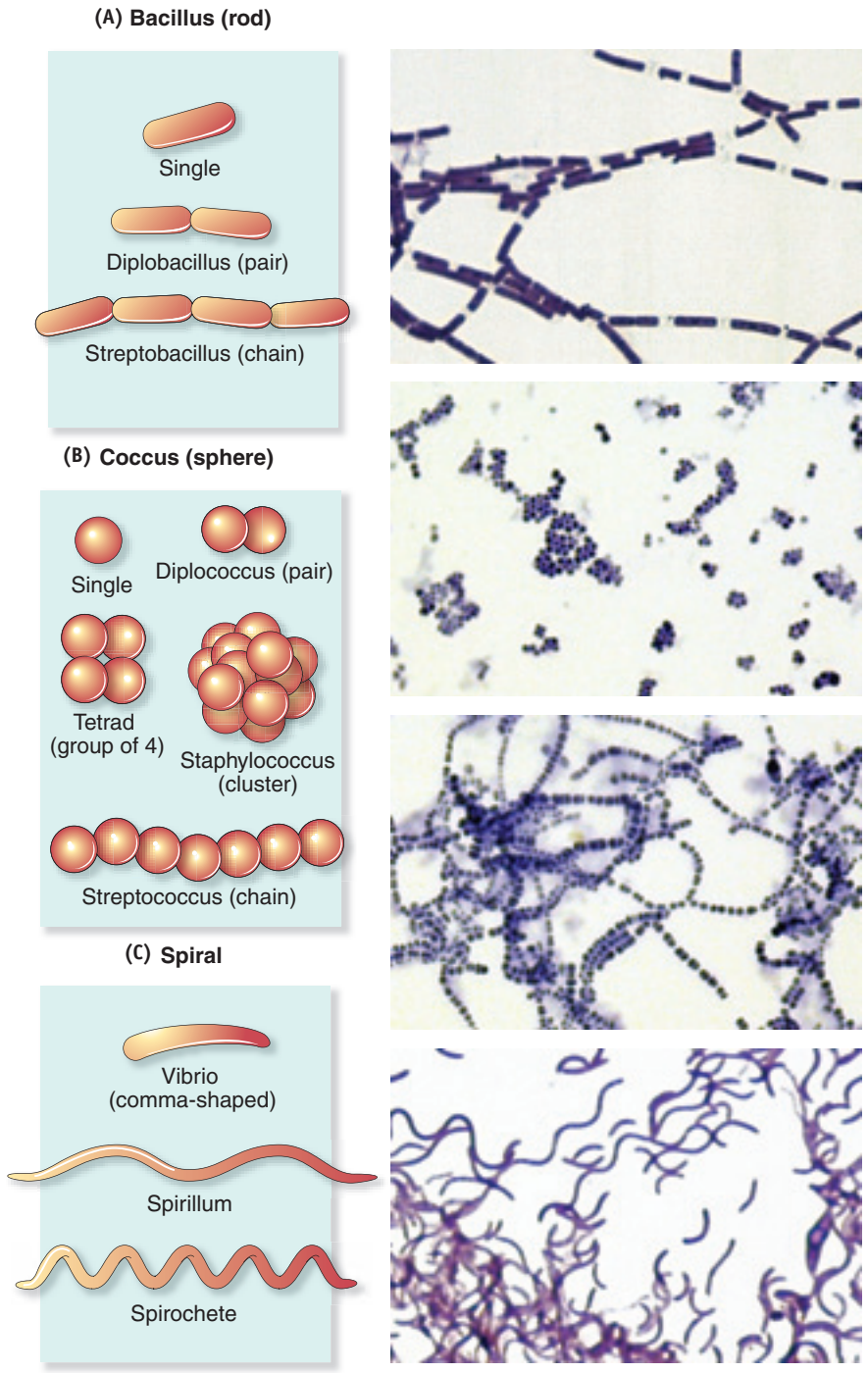


FIGURE 4.5 Variation in Shape and Cell Arrangements. Many bacterial and archaeal cells have a bacillus (**A**) or coccus (**B**) shape. Most spiral shaped-cells (**C**) are not organized into a specific arrangement. »» In photomicrograph (C), identify the vibrio and the spirillum forms.

lococcus" can be used to describe cell shape and arrangement, or a bacterial genus (*Streptococcus* and *Staphylococcus*).

The third common shape of bacterial cells is the **spiral**, which can take one of three forms (FIGURE 4.5C). The **vibrio** is a curved rod that resembles a comma. The cholera-causing organism *Vibrio cholerae* is typical. Another spiral form called **spirillum** (pl., spirilla) has a helical shape with a thick, rigid cell wall and flagella that assist movement. The spiral-shaped form known as **spirochete** has a thin, flexible cell wall but no flagella

in the traditional sense. Movement in these organisms occurs by contractions of endoflagella that run the length of the cell. The organism causing syphilis, *Treponema pallidum,* typifies a spirochete. Spiral-shaped bacterial cells can be from 1 µm to 100 µm in length.

In addition to the bacillus, coccus, and spiral shapes, other variations exist. Some bacterial species have appendaged bacterial cells while others consist of branching filaments; and some archaeal species have square and star shapes.

CONCEPT AND REASONING CHECKS

4.3 Propose a reason why bacilli do not form tetrads or clusters.

4.3 An Overview to Bacterial and Archaeal Cell Structure

In the last chapter we discovered that bacterial and archaeal cells appear to have little visible structure when observed with a light microscope. This, along with their small size, gave the impression they are homogeneous, static structures with an organization very different from eukaryotic cells.

However, the point was made that bacterial and archaeal species still have all the complex processes typical of eukaryotic cells. It is simply a matter that, in most cases, the structure and sometimes pattern to accomplish these processes is different from the membranous organelles typical of eukaryotic species.

Cell Structure Organizes Cell Function

KEY CONCEPT

4. Bacterial and archaeal cells are organized at the cellular and molecular levels.

Recent advances in understanding bacterial and archaeal cell biology indicate these organisms exhibit a highly ordered intracellular organization. This organization is centered on three specific processes that need to be carried out (FIGURE 4.6). These are:

- **Sensing and responding to the surrounding environment.** Because most bacterial and archaeal cells are surrounded by a cell wall, some pattern of "external structures" is necessary to sense their environment and respond to it or other cells.
- **Compartmentation of metabolism.** As described in Chapter 3, cell metabolism must be segregated from the exterior environment and yet be able to transport materials to and from that environment.

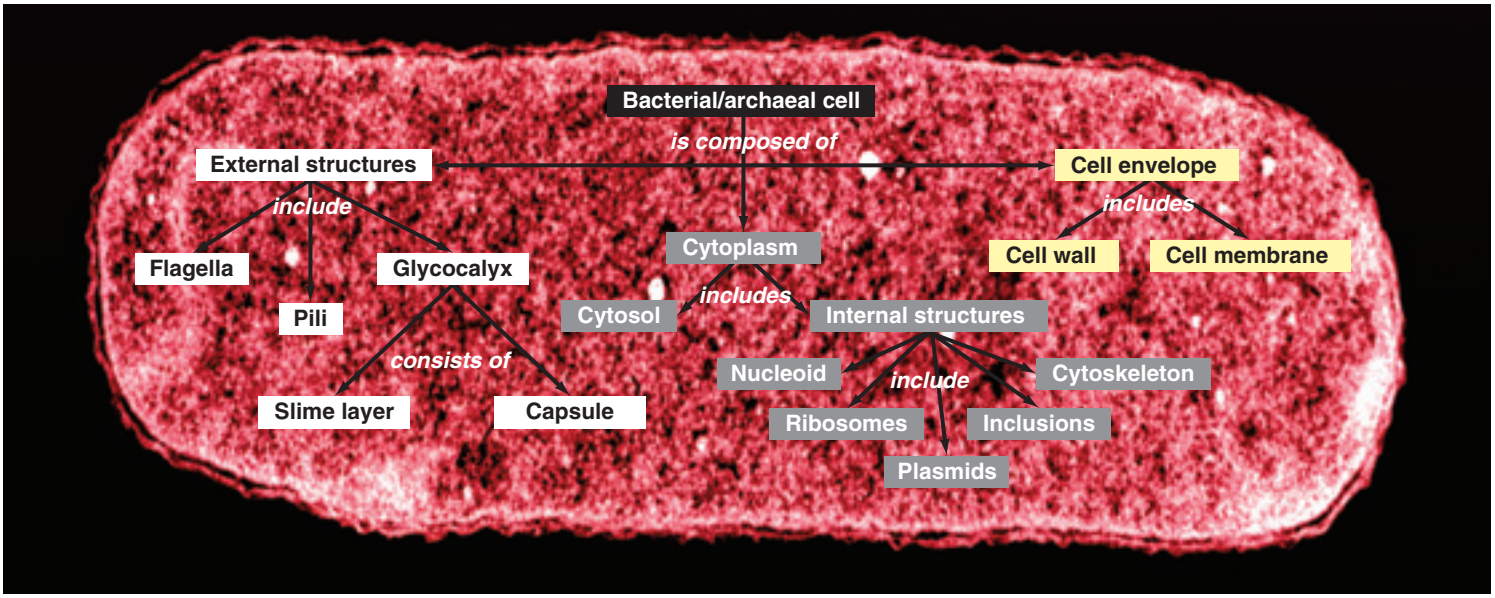


FIGURE 4.6 **A Concept Map for Studying Bacterial and Archaeal Cell Structure.** Not all cells have all the structures shown here. »» Why can't we see in the TEM image of a bacterial cell all the structures outlined in the concept map?

In addition, protection from osmotic pressure due to water movement into cells must be in place. The "cell envelope" fulfills those roles.

- **Growth and reproduction.** Cell survival demands a complex metabolism that occurs within the aqueous "cytoplasm." These processes and reproduction exist as internal structures or subcompartments localized to specific areas within the cytoplasm.

Our understanding of bacterial and archaeal cell biology is still an emerging field of study. However, there is more to cell structure than previously thought—smallness does not equate with simplicity.

Although this chapter is primarily looking at bacterial cells at the cellular level, it also is important to realize that bacterial and archaeal cells, like their eukaryotic counterparts, are organized on the molecular level as well. Specific cellular proteins can be localized to specific regions of the cell. For example, as the name suggests, *Streptococcus pyogenes* has spherical cells. Yet many of the proteins that confer its pathogenic nature in causing diseases like strep throat are secreted from a specific area of the surface. *Yersinia pestis,* which is the agent responsible for plague, contains a specialized secretion apparatus through which proteins are released. This apparatus only exists on the bacterial surface that is in contact with the target human cells.

So, the cell biology studies are not only important in their own right in understanding cell structure, these studies also may have important significance to clinical microbiology and the fight against infectious disease. As more is discovered about these cells and how they truly differ from eukaryotic cells, the better equipped we will be to develop new antimicrobial agents that will target the subcellular organization of pathogens. In an era when we have fewer effective antibiotics to fight infections, the application of the understanding of cell structure and function may be very important.

On the following pages, we examine some of the common structures found in an idealized bacterial cell, as no single species contains all the structures (FIGURE 4.7). Our journey starts by examining the structures on or extending from

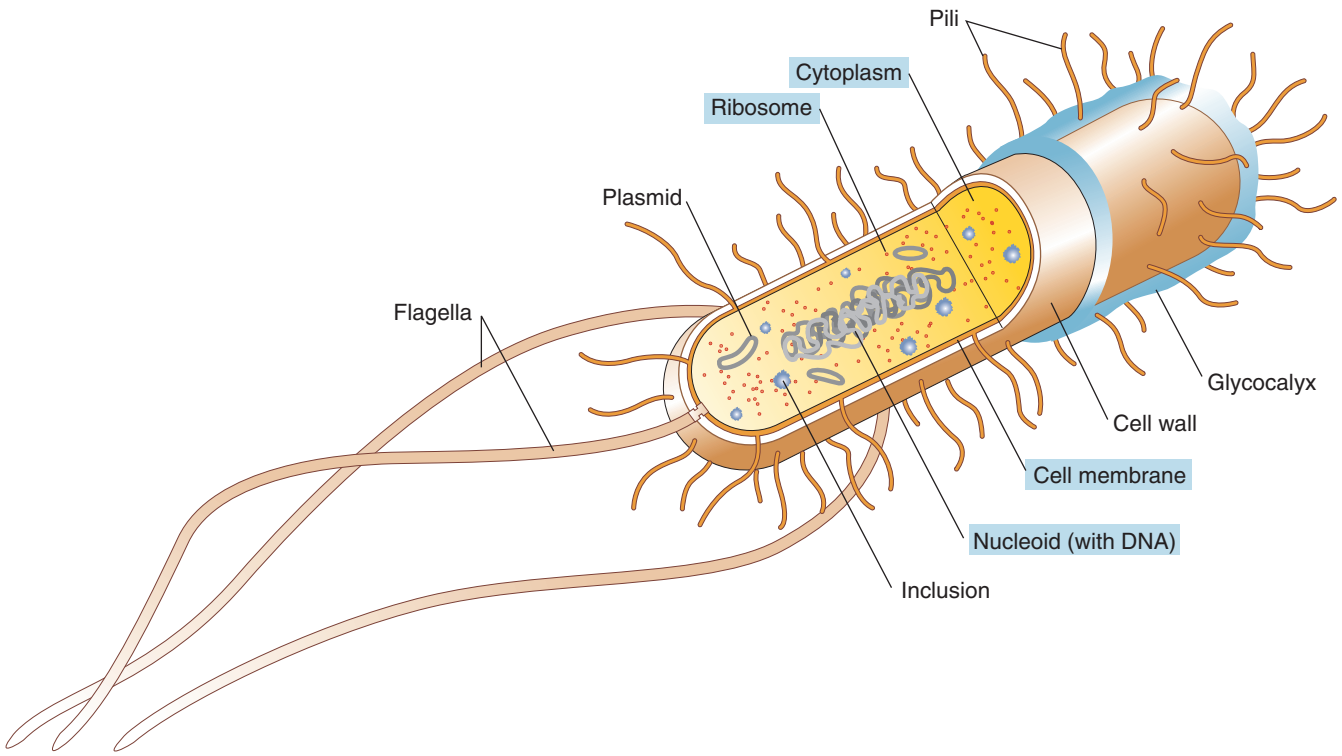


FIGURE 4.7 **Bacterial Cell Structure.** The structural features of a composite, "idealized" bacterial cell. Structures highlighted in blue are found in all bacterial and archaeal species. »» Which structures represent (a) external structures, (b) the cell envelope, and (c) cytoplasmic structures?

the surface of the cell. Then, we examine the cell envelope and spend some time discussing the cell membrane. Our journey then plunges into the cell cytoplasm. All cells must control and coordinate many metabolic processes that need to be separated from one another. We will discover the cytoplasmic subcellular compartmentation that provides this function.

CONCEPT AND REASONING CHECKS

4.4 What is gained by bacterial and archaeal cells being organized into three general sets of structures—external, envelope, and cytoplasmic?

4.4 External Cell Structures

Bacterial and archaeal cells need to respond to and monitor their external environment. This is made difficult by having a cell wall that "blindfolds" the cell. Many cells have solved this sensing problem by possessing structures that extend from the cell surface into the environment.

Mucosal: Referring to the mucous membranes lining many body cavities exposed to the environment.

Virulence factor: A pathogen-produced molecule or structure that allows the cell to invade or evade the immune system and possibly cause disease.

Pili Are Protein Fibers Extending from the Cell Surface

KEY CONCEPT

5. Pili allow cells to attach to surfaces or other cells.

Numerous short, thin fibers, called **pili** (sing., pilus; *pilus* = "hair"), protrude from the surface of most gram-negative bacteria (FIGURE 4.8). The rigid fibers, composed of protein, act as scaffolding onto which specific adhesive molecules, called **adhesins**, are attached. Therefore, the function of pili is to attach cells to surfaces forming biofilms or, in the case of human pathogens, on human cell and tissue surfaces. This requires that the pili on different bacterial species have specialized adhesins to "sense" the appropriate cell. For example, the pili adhesins on *Neisseria gonorrhoeae* cells specifically anchor the cells to the mucosal surface of the urogenital tract whereas the adhesins on *Bordetella pertussis* (causative agent of whooping cough) adhere to cells of the mucosal surface of the upper respiratory tract. In this way, the pili act as a virulence factor by enhancing attachment to host cells, facilitating tissue colonization, and possibly leading to disease development. Without the chemical mooring line lashing the bacterial cells to host cells, it is less likely the cells could infect host tissue (MicroFocus 4.2).

Besides these attachment pili, some bacterial species produce flexible **conjugation pili** that establish contact between appropriate cells, facilitating the transfer of genetic material from donor to recipient through a process called conjugation (Chapter 9). Conjugation pili are longer than attachment pili and only one or a few are produced on a cell.

Until recently, attachment pili were thought to be specific to only certain species of gram-negative bacteria. However, research now indicates that extremely thin pili are present on at least some gram-positive bacteria, including the pathogen *Corynebacterium diphtheriae* and *Streptococcus* species. However, very little is known about their function, although they probably play a very similar role to the pili on gram-negative cells.

It should be noted that microbiologists often use the term "pili" interchangeably with "fimbriae" (sing., fimbria; *fimbria* = "fiber").

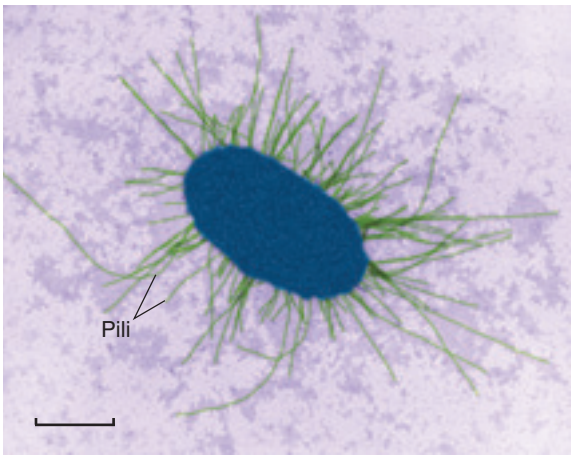


FIGURE 4.8 Bacterial Pili. False-color transmission electron micrograph of an *Escherichia coli* cell (blue) with many pili (green). (Bar = 0.5 µm.) »» What function do pili play?

CONCEPT AND REASONING CHECKS

4.5 What would happen if pili lacked adhesins?

Flagella Are Long Appendages Extending from the Cell Surface

KEY CONCEPT

6. Flagella provide motility.

MICROFOCUS 4.2: Public Health
Diarrhea Doozies

They gathered at the clinical research center at Stanford University to do their part for the advancement of science (and earn a few dollars as well). They were the "sensational sixty"—sixty young men and women who would spend three days and nights and earn $300 to help determine whether hair-like structures called pili have a significant place in disease.

A number of nurses and doctors were on hand to help them through their ordeal. The students would drink a fruit-flavored cocktail containing a special diarrhea-causing strain of *Escherichia coli*. Thirty cocktails had *E. coli* with normal pili, while thirty had *E. coli* with pili mutated beyond repair. The hypothesis was that the bacterial cells with normal pili would latch onto intestinal tissue and cause diarrhea, while those with mutated pili would be unable to attach and would be swept away by the rush of intestinal movements and not cause intestinal distress. At least that's what the sensational sixty would either verify or prove false.

On that fateful day in 1997, the experiment began. Neither the students nor the health professionals knew who was drinking the diarrhea cocktail and who was getting the "free pass"; it was a so-called double-blind experiment. Then came the waiting. Some experienced no symptoms, but others felt the bacterial onslaught and clutched at their last remaining vestiges of dignity. For some, it was three days of hell, with nausea, abdominal cramps, and numerous bathroom trips; for others, luck was on their side, and investing in a lottery ticket seemed like a good idea.

When it was all over, the numbers appeared to bear out the hypothesis: The great majority of volunteers who drank the mutated bacterial cells experienced no diarrhea, while the great majority of those who drank the normal bacterial cells had attacks of diarrhea, in some cases real doozies.

All appeared to profit from the experience: The scientists had some real-life evidence that pili contribute to infection; the students made their sacrifice to science and pocketed $300 each; and the local supermarket had a surge of profits from unexpected sales of toilet paper, Pepto-Bismol, and Imodium.

Numerous species in the domains *Bacteria* and *Archaea* are capable of some type of locomotion. This can be in the form of flagellar motility or gliding motility.

Flagellar Motility. Many bacterial and archaeal cells are motile by using remarkable "nanomachines" called **flagella** (sing., flagellum). Depending on the species, one or more flagella may be attached to one or both ends of the cell, or at positions distributed over the cell surface (FIGURE 4.9A).

Flagella range in length from 10 µm to 20 µm and are many times longer than the diameter of the cell. Because they are only about 20 nm thick, they cannot be seen with the light microscope unless stained. However, their existence can be inferred by using dark-field microscopy to watch the live cells dart about.

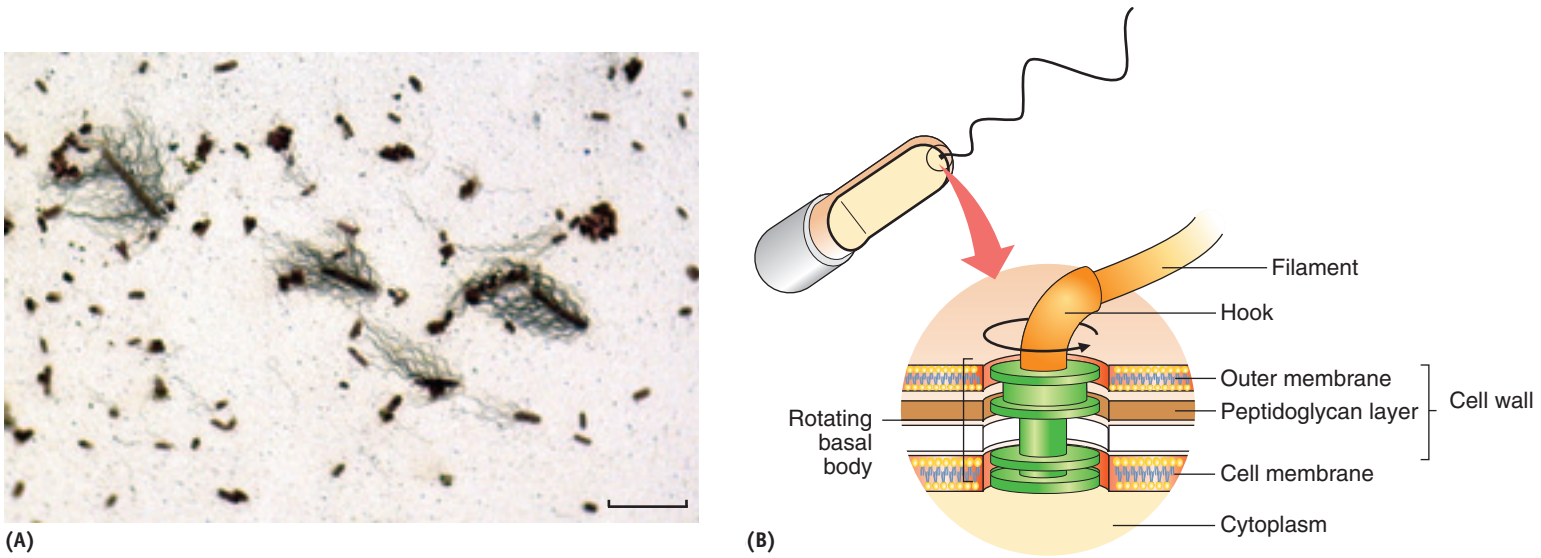
In the domain *Bacteria*, each flagellum is composed of a helical filament, hook, and basal body (FIGURE 4.9B). The hollow filament is composed of long, rigid strands of protein while the hook attaches the filament to a basal body anchored in the cell membrane and cell wall.

The basal body is an assembly of more than 20 different proteins that form a central rod and set of enclosing rings. Gram-positive bacteria have a pair of rings embedded in the cell membrane and one in the cell wall, while gram-negative bacteria have a pair of rings embedded in the cell membrane and another pair in the cell wall.

In the domain *Archaea*, flagellar protein composition and structure differs from that of the *Bacteria*; motility appears similar though.

The basal body represents a powerful biological motor or rotary engine that generates a propeller-type rotation of the flagellum. The energy for rotation comes from the diffusion of protons (hydrogen ions; H^+) into the cell through proteins associated with the basal body. This energy is sufficient to produce up to 1,500 rpm by the filament, driving the cell forward.

What advantage is gained by cells having flagella? In nature, there are many chemical nutrients in the environment that cells need to survive. Cells will move toward such **attractants** by using their flagella to move up the concentration gradient; that is, toward the attractant. The process is called **chemotaxis**.



(A) (B)

FIGURE 4.9 Bacterial Flagella. (**A**) A light micrograph of *Proteus vulgaris* showing numerous flagella extending from the cell surface. (Bar = 10 µm.) Note that the length of a flagellum is many times the width of the cell. (**B**) The flagellum on a gram-negative bacterial cell is attached to the cell wall and membrane by two pairs of protein rings in the basal body. »» Why is the flagellum referred to as a "nanomachine"?

Temporal sensing: One that compares the chemical environment and concentration from one moment to the next.

Being so small, the cells sense their chemical surroundings using a temporal sensing system. In the absence of a gradient, the flagella all rotate as a bundle counterclockwise and the cell moves straight ahead in short bursts called "runs" (FIGURE 4.10A). These runs can last a few seconds and the cells can move up to 10 body lengths per second (the fastest human can run about 5–6 body lengths per second). A reversal of flagellar rotation (clockwise rotation) causes the cell to "tumble" randomly for a second as the flagella become unbundled. Then, the motor again reverses direction and another run occurs in a new direction.

If an attractant gradient is present, cell behavior changes; cells moving up the gradient now experience longer periods when the motor turns counterclockwise (lengthened runs) and shorter periods when it turns clockwise (shortened tumbles) (FIGURE 4.10B). The combined result is a net movement toward the attractant; that is, up the concentration gradient.

Similar types of motile behavior are seen in photosynthetic organisms moving toward light (phototaxis) or other cells moving toward oxygen gas (aerotaxis). MicroFocus 4.3 investigates how flagella may have evolved.

One additional type of flagellar organization is found in the spirochetes, a group of gram-negative, coiled bacterial species. The cells are motile by flagella that extend from one or both poles of the cell but fold back along the cell body (FIGURE 4.11). Such **endoflagella** and the cell body are surrounded by an outer sheath membrane. Motility results from the torsion generated on the cell by the normal rotation of the flagella. The resulting motility is less regular and more jerky than with flagellar motility.

Gliding Motility. Some bacterial cells can move about without flagella by gliding across a solid surface. The motility occurs along the long axis of bacillus- or filamentous-shaped cells and usually is slower than flagellar motility. The cyanobacteria and myxobacteria (see Chapter 3) are two examples of organisms with gliding motility.

How the cells actually move is not completely understood. It appears that the force for gliding is generated by cytoplasmic proteins (motor proteins) that move along a helical track pushing the cell forward.

CONCEPT AND REASONING CHECKS

4.6 Explain how flagella move cells during a "run."

The Glycocalyx Is an Outer Layer External to the Cell Wall

KEY CONCEPT

7. A glycocalyx protects against desiccation, attaches cells to surfaces, and helps pathogens evade the immune system.

Many bacterial species secrete an adhering layer of polysaccharides, or polysaccharides and small

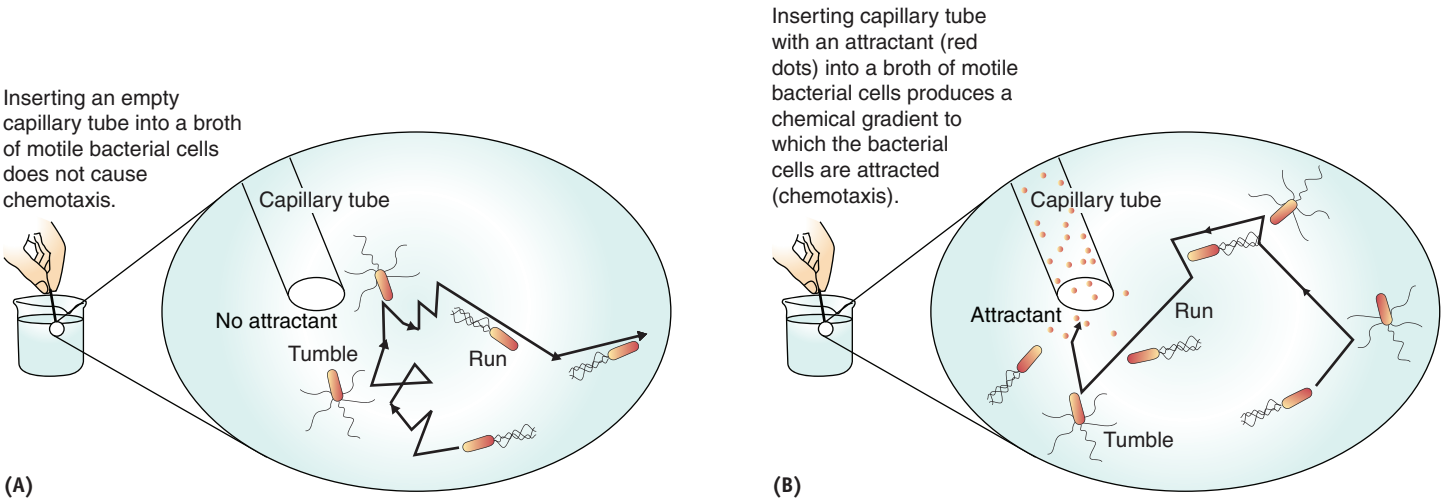


FIGURE 4.10 Chemotaxis. Chemotaxis represents a behavioral response to chemicals. (**A**) Rotation of the flagellum counterclockwise causes the bacterial cell to " run," while rotation of the flagellum clockwise causes the bacterial cell to "tumble," as shown. (**B**) During chemotaxis to an attractant, such as sugar, flagellum behavior leads to longer runs and fewer tumbles, which will result in biased movement toward the attractant. »» Predict the behavior of a bacterial cell if it sensed a repellant; that is a potential harmful or lethal chemical.

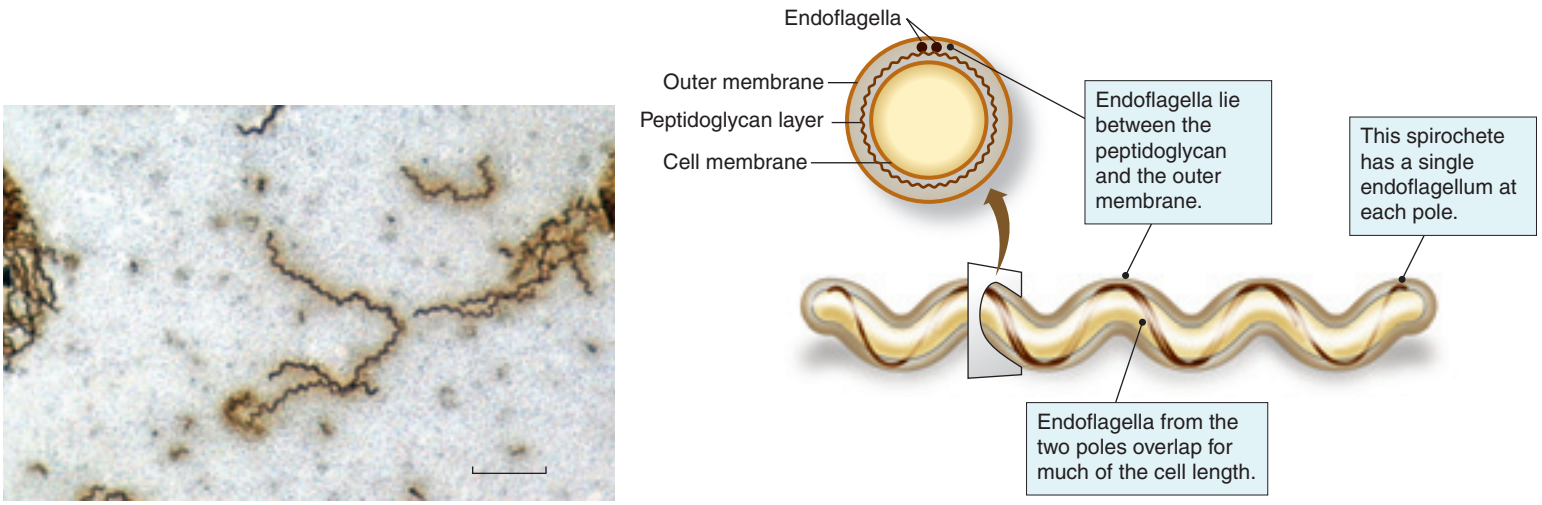


FIGURE 4.11 The Spirochete Endoflagella. (**A**) A light micrograph of *Treponema pallidum* shows the corkscrew-shaped spirochete cell. (Bar = 10 µm.) (**B**) Diagram showing the positioning of endoflagella in a spirochete. »» How are endoflagella different from true bacterial flagella?

proteins, called the **glycocalyx** (*glyco* = "sweet"; *calyx* = "coat"). The layer can be thick and covalently bound to the cell, in which case it is known as a **capsule**. A thinner, loosely attached layer is referred to as a **slime layer**. Colonies containing cells with a glycocalyx appear moist and glistening. The actual capsule can be seen by light microscopy when observing cells in a negative stain preparation or by transmission electron microscopy (FIGURE 4.12).

The glycocalyx serves as a buffer between the cell and the external environment. Because of its high water content, the glycocalyx can protect cells from desiccation. Another major role of the glycocalyx is to allow the cells to attach to surfaces. The glycocalyx of *V. cholerae*, for example, permits the cells to attach to the intestinal wall of the host. The glycocalyx of pathogens therefore represents another virulence factor.

Other encapsulated pathogens, such as *Streptococcus pneumoniae* (a principal cause of bacterial pneumonia) and *Bacillus anthracis*, evade the immune system because they cannot be easily engulfed by white blood cells during phagocytosis. Scientists believe the repulsion between bacterial cell and phagocyte is due to strong negative charges on the capsule and phagocyte surface.

Encapsulated: A cell having a capsule.

Phagocytosis: A process whereby certain white blood cells (phagocytes) engulf foreign matter and often destroy microorganisms.

MICROFOCUS 4.3: Evolution

The Origin of the Bacterial Flagellum

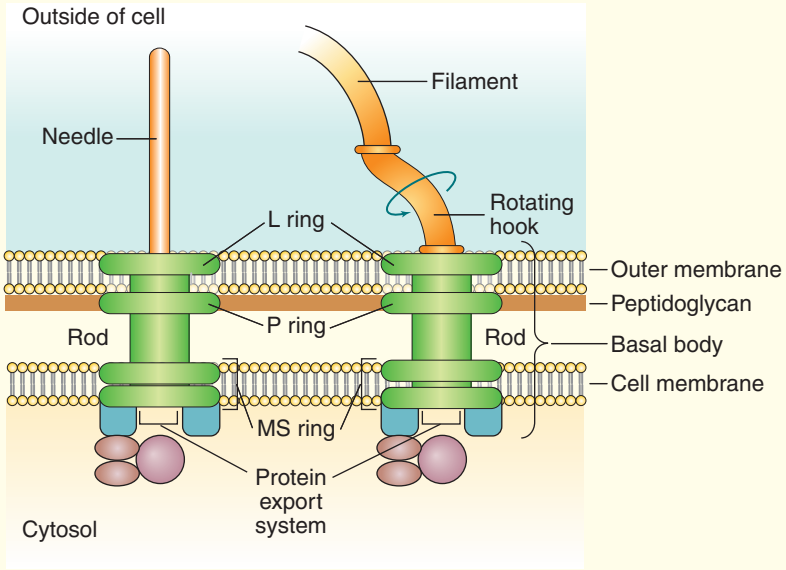
Flagella are an assembly of protein parts forming a rotary engine that, like an outboard motor, propel the cell forward through its moist environment. Recent work has shown how such a nanomachine may have evolved.

Several bacterial species, including *Yersinia pestis,* the agent of bubonic plague, contain structures to inject toxins into an appropriate eukaryotic host cell. These bacterial cells have a hollow tube or needle to accomplish this process, just as the bacterial flagellum and filament are hollow (see diagram below). In addition, many of the flagellar proteins are similar to part of the injection proteins. In 2004, investigations discovered that *Y. pestis* cells actually contain all the genes needed for a flagellum—but the cells have lost the ability to use these genes. *Y. pestis* is nonmotile and it appears that the cells use a subset of the flagellar proteins to build the injection device.

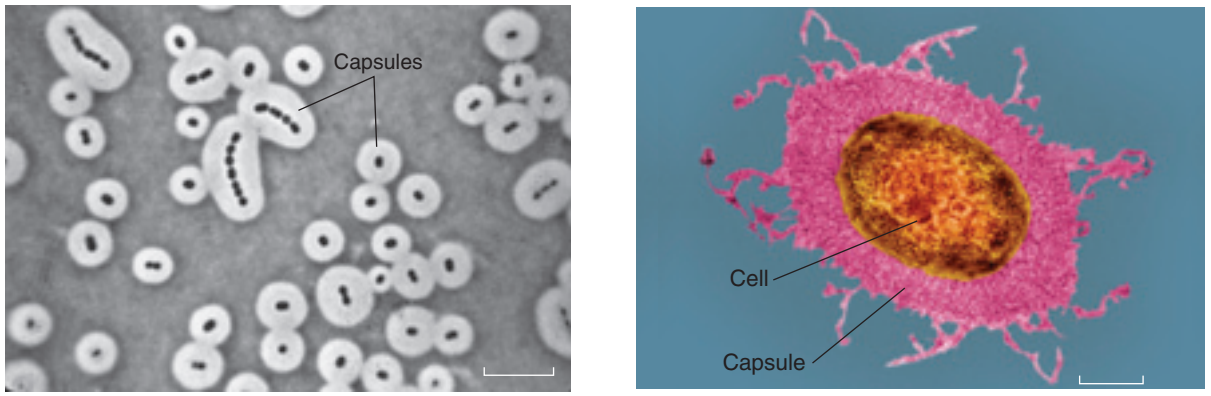
One scenario then is that an ancient cell evolved a structure that was the progenitor of the injection and flagellar systems. In fact, many of the proteins in the basal body of flagellar and injection systems are similar to proteins involved in proton (hydrogen ion; H^+) transport. Therefore, a proton transport system may have evolved into the injection device and, through diversification events, evolved into the motility structure present on many bacterial cells today.

The fascinating result of these investigations and proposals is it demonstrates that structures can evolve from other structures with a different function. It is not necessary that evolution "design" a structure from scratch but rather it can modify existing structures for other functions.

Individuals have proposed that the complexity of structures like the bacterial flagellum are just too complex to arise gradually through a step-by-step process. However, the investigations being conducted illustrate that a step-by-step evolution of a specific structure is not required. Rather, there can be cooperation, where one structure is modified to have other functions. The bacterial flagellum almost certainly falls into that category.



A bacterial injection device (left) compared to a bacterial flagellum (right). Both have a protein export system in the base of the basal body.



(A) (B)

FIGURE 4.12 The Bacterial Glycocalyx. (**A**) Demonstration of the presence of a capsule in an *Acinetobacter* species by negative staining and observed by phase-contrast microscopy. (Bar = 10 µm.) (**B**) A false-color transmission electron micrograph of *Escherichia coli*. The cell is surrounded by a thick capsule (pink). (Bar = 0.5 µm.) »» How does the capsule provide protection for the bacterial cell?

A slime layer usually contains a mass of tangled fibers of a polysaccharide called dextran (see Chapter 2). The fibers attach the bacterial cell to tissue surfaces. A case in point is *Streptococcus mutans*, an important cause of tooth decay previously discussed in MicroFocus 2.4. This species forms dental plaque, which represents a type of biofilm on the tooth surface. TEXTBOOK CASE 4 (p. 116) details a medical consequence of a biofilm.

CONCEPT AND REASONING CHECKS

4.7 Under what circumstances might it be advantageous to a bacterial cell to have a capsule rather than a slime layer?

4.5 The Cell Envelope

The **cell envelope** is a complex structure that forms the two "wrappers"—the **cell wall** and the **cell membrane**—surrounding the cell cytoplasm. The cell wall is relatively porous to the movement of substances whereas the cell membrane regulates transport of nutrients and metabolic products.

The Bacterial Cell Wall Is a Tough and Protective External Shell

KEY CONCEPT

8. Bacterial cell walls help maintain cell shape and protect the cell membrane from rupture.

The fact that most all bacterial and archaeal cells have a cell wall suggests the critical role this structure must play. By covering the entire cell surface, the cell wall acts as an exoskeleton to protect the cell from injury and damage. It helps, along with the cytoskeleton (see Section 4.6), to maintain the shape of the cell and reinforce the cell envelope against the high intracellular water (osmotic) pressure pushing against the cell membrane. As described in Chapter 3, most microbes live in an environment where there are more dissolved materials inside the cell than outside. This hypertonic condition in the cell means water diffuses inward, accounting for the increased osmotic pressure. Without a cell wall, the cell would rupture or undergo **lysis** (FIGURE 4.13). It is similar to blowing so much air into a balloon that the air pressure bursts the balloon.

Hypertonic: A solution with more dissolved material (solutes) than the surrounding solution.

The bacterial cell wall differs markedly from the walls of archaeal cells and cells of eukaryotic

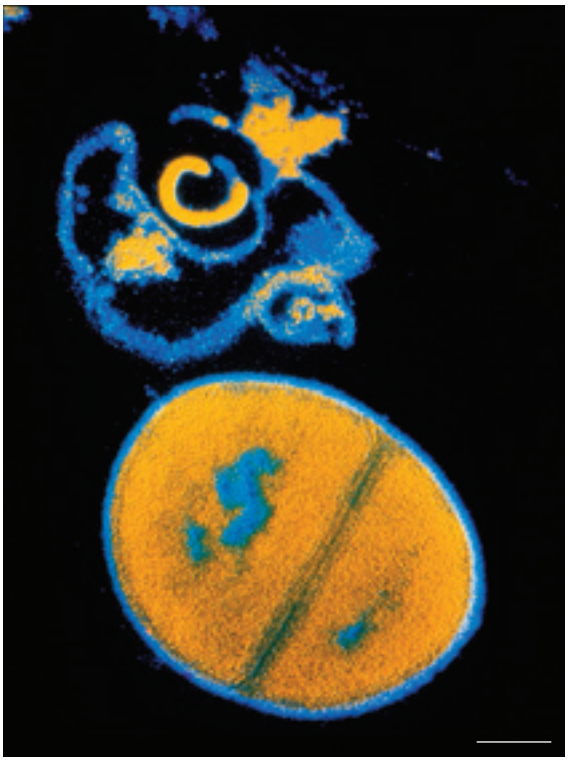


FIGURE 4.13 Cell Rupture (Lysis). A false-color electron micrograph showing the lysis of a *Staphylococcus aureus* cell. The addition of the antibiotic penicillin interferes with the construction of the peptidoglycan in new cells, and they quickly burst (top cell). (Bar = 0.25 µm.)
»» Where is the concentration of dissolved substances (solutes) higher, inside the cell or outside? Explain how this leads to cell lysis.

Autolytic enzymes: Enzymes that break bonds in the peptidoglycan, thereby causing lysis of the cell.

microorganisms (algae and fungi) in containing **peptidoglycan**, which is a network of disaccharide chains (glycan strands) cross-linked by short peptides (FIGURE 4.14A). Each disaccharide in this very large molecule is composed of two monosaccharides, N-acetylglucosamine (NAG) and N-acetylmuramic acid (NAM) (see Chapter 2). The carbohydrate backbone can occur in multiple layers connected by side chains of four amino acids and peptide cross-bridges.

There is more to a bacterial cell wall than just peptidoglycan, so several forms of cell wall architecture exist.

Gram-Positive Walls. Most gram-positive bacterial cells have a very thick, rigid peptidoglycan cell wall (FIGURE 4.14B). The abundance and thickness (25 nm) of this material may be one reason why they retain the crystal violet in the Gram stain (see Chapter 3). The multiple layers of glycan strands are cross-linked to one another both in the same layer as well as between layers.

Endotoxin: A poison that can activate inflammatory responses, leading to high fever, shock, and organ failure.

The gram-positive cell wall also contains a sugar-alcohol called **teichoic acid**. Wall teichoic acids, which are bound to the glycan chains, are essential for cell viability—if the genes for teichoic acid synthesis are deleted, cell death occurs. Still, the function of the teichoic acids remains unclear. They may help maintain a surface charge on the cell wall, control the activity of autolytic enzymes acting on the peptidoglycan, and/or maintain permeability of the cell wall layer.

The bacterial genus *Mycobacterium* is phylogenetically related to the gram-positive bacteria. However, these rod-shaped cells have evolved another type of wall architecture to protect the cell membrane from rupture. The cell wall is composed of a waxy lipid called **mycolic acid** that is arranged in two layers that are covalently attached to the underlying peptidoglycan. Such a hydrophobic layer is impervious to the Gram stains, so stain identification of *M. tuberculosis* is carried out using the acid-fast stain procedure (see Chapter 3).

Gram-Negative Walls. The cell wall of gram-negative bacterial cells is structurally quite different from that of the gram-positive wall (FIGURE 4.14C). The peptidoglycan layer is two-dimensional; the glycan strands compose just a single layer or two. This is one reason why it loses the crystal violet dye during the Gram stain. Also, there is no teichoic acid present.

The unique feature of the gram-negative cell wall is the presence of an **outer membrane**, which is separated by a gap, called the **periplasm**, from the cell membrane. This gel-like compartment contains digestive enzymes and transport proteins to speed entry of nutrients into the cell. The peptidoglycan layer is located in the periplasm and attached to lipoproteins in the cell membrane.

The inner half of the outer membrane contains phospholipids similar to the cell membrane. However, the outer half is composed primarily of **lipopolysaccharide (LPS)**, which consists of polysaccharide attached to a unique lipid molecule known as **lipid A**. The so-called O polysaccharide is used to identify variants of a species (e.g., strain O157:H7 of *E. coli*). On cell death, lipid A is released and represents an endotoxin that can be toxic if ingested (Chapter 19).

The outer membrane also contains unique proteins called **porins**. These proteins form pores in the outer membrane through which small,

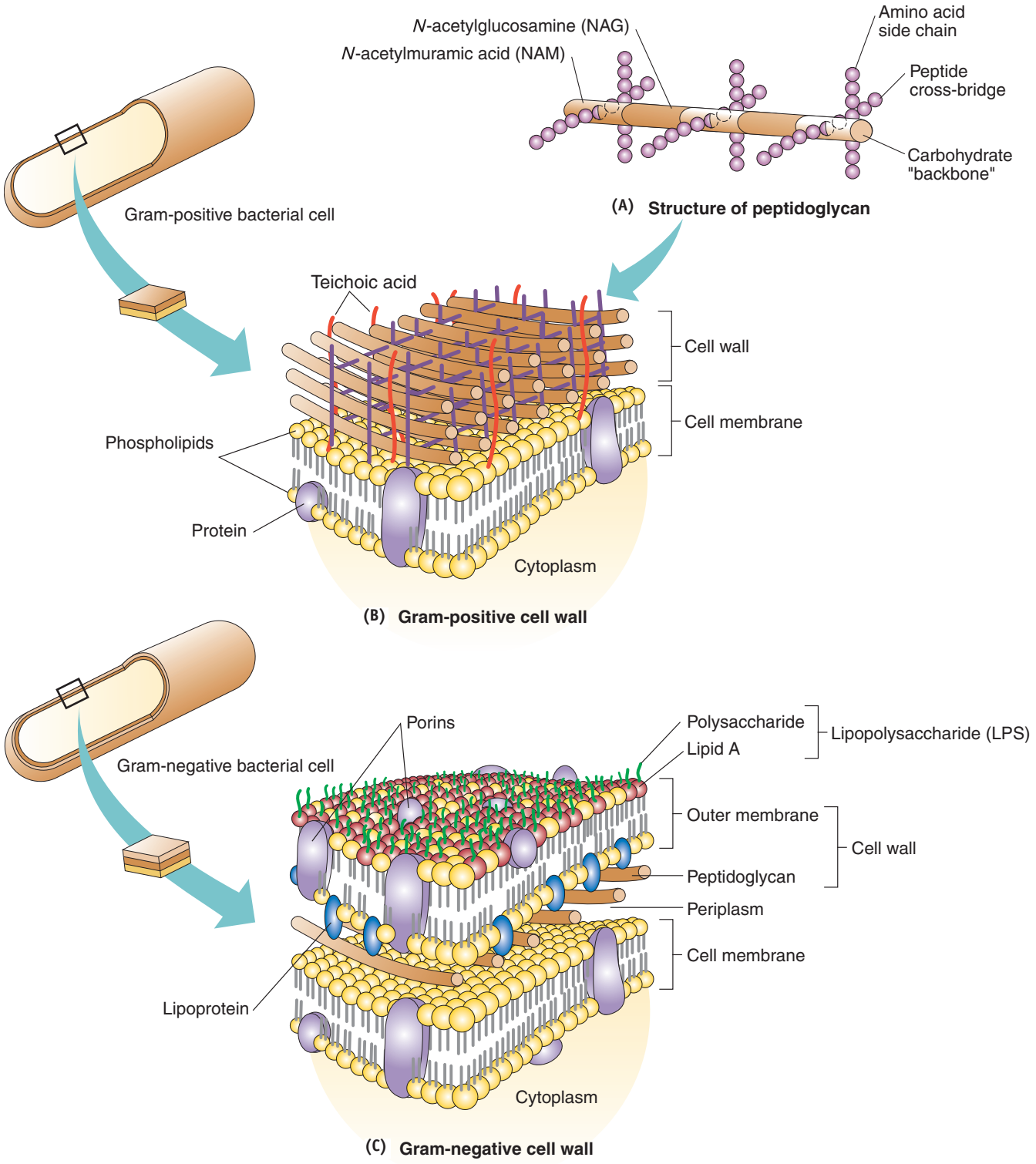


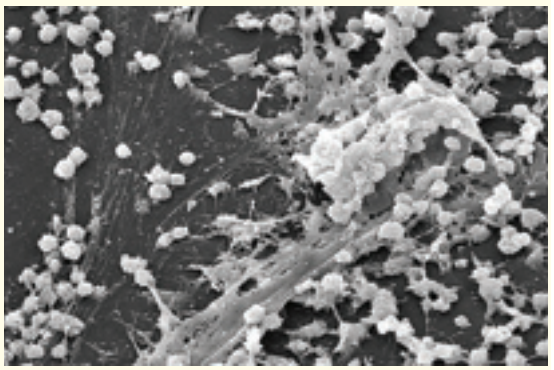
FIGURE 4.14 **A Comparison of the Cell Walls of Gram-Positive and Gram-Negative Bacterial Cells.** (**A**) The structure of peptidoglycan is shown as units of NAG and NAM joined laterally by amino acid cross-bridges and vertically by side chains of four amino acids. (**B**) The cell wall of a gram-positive bacterial cell is composed of peptidoglycan layers combined with teichoic acid molecules. (**C**) In the gram-negative cell wall, the peptidoglycan layer is much thinner, and there is no teichoic acid. Moreover, an outer membrane overlies the peptidoglycan layer such that both comprise the cell wall. Note the structure of the outer membrane in this figure. It contains porin proteins and the outer half is unique in containing lipopolysaccharide. »» Simply based on cell wall structure, assess the potential of gram-positive and gram-negative cells as pathogens.

Textbook CASE 4

An Outbreak of *Enterobacter cloacae* Associated with a Biofilm

Hemodialysis is a treatment for people with severe chronic kidney disease (kidney failure). The treatment filters the patient's blood to remove wastes and excess water. Before a patient begins hemodialysis, an access site is created on the lower part of one arm. Similar to an intravenous (IV) site, a tiny tube runs from the arm to the dialysis machine. The patient's blood is pumped through the dialysis machine, passed through a filter or artificial kidney called a dialyzer, and the cleaned blood returned to the patient's body at the access site. The complete process can take 3 to 4 hours.

1. During September 1995, a patient at an ambulatory hemodialysis center in Montreal, Canada received treatment on a hemodialysis machine to help relieve the effects of kidney disease. The treatment was performed without incident.
2. The next day, a second patient received treatment on the same hemodialysis machine. His treatment also went normally, and he returned to his usual activities after the session was completed.
3. In the following days, both patients experienced bloodstream infections (BSIs). They had high fever, muscular aches and pains, sore throat, and impaired blood circulation. Because the symptoms were severe, the patients were hospitalized. Both patients had infections of *Enterobacter cloacae,* a gram-negative rod.
4. In the following months, an epidemiological investigation reviewed other hemodialysis patients at that center. In all, seven additional adult patients were identified who had used the same hemodialysis machine. They discovered all seven had similar BSIs.
5. Inspection of the hemodialysis machine used by these nine patients indicated the presence of biofilms containing *Enterobacter cloacae,* which was identical to those samples taken from the patients' bloodstreams (see figure).
6. Further study indicated that the dialysis machine was contaminated with *E. cloacae,* specifically where fluid flows.
7. It was discovered that hospital personnel were disinfecting the machines correctly. The problem was that the valves in the drain line were malfunctioning, allowing a backflow of contaminated material.
8. Health officials began a hospital education program to ensure that further outbreaks of infection would be minimized.



Similar to the description in this textbook case, biofilms consisting of *Staphylococcus* cells can contaminate hemodialysis machines.

Questions:

(Answers can be found in Appendix D.)

A. Suggest how the hemodialysis machine originally became contaminated.

B. Why weren't the other five cases of BSI correlated with the hemodialysis machine until the epidemiological investigation was begun?

C. How could future outbreaks of infection be prevented?

For additional information see http://www.cdc.gov/mmwr/preview/mmwrhtml/00051244.htm.

TABLE **4.2** A Comparison of Gram-Positive and Gram-Negative Cell Walls

Characteristic	Gram Positive	Gram Negative
Peptidoglycan	Yes, thick layer	Yes, thin layer
Teichoic acids	Yes	No
Outer membrane	No	Yes
Lipopolysaccharides (LPS)	No	Yes
Porin proteins	No	Yes
Periplasm	No	Yes

hydrophilic molecules (sugars, amino acids, some ions) pass into the periplasm. Larger, hydrophobic molecules cannot pass, partly accounting for the resistance of gram-negative cells to many antimicrobial agents, dyes, disinfectants, and lysozyme.

Before leaving the bacterial cell walls, a brief mention should be made of bacterial species that lack a cell wall. The mycoplasmas are a wall-less genus that is again phylogenetically related to the gram-positive bacteria. Taxonomists believe that the mycoplasmas once had a cell wall but lost it because of their parasitic relationship with their host. To help protect the cell membrane from rupture, the mycoplasmas are unusual in containing sterols in the cell membrane (see Chapter 2).

TABLE 4.2 summarizes the major differences between the two major types of bacterial cell walls.

CONCEPT AND REASONING CHECKS

4.8. Penicillin and lysozyme primarily affect peptidoglycan synthesis in gram-positive bacterial cells. Why are these agents less effective against gram-negative bacterial cells?

The Archaeal Cell Wall Also Provides Mechanical Strength

KEY CONCEPT

9. Archaeal cell walls have crystalline layers.

Archaeal species vary in the type of wall they possess. None have the peptidoglycan typical of the *Bacteria*. Some species have a **pseudopeptidoglycan** where the NAM is replaced by N-acetyltalosamine uronic acid (NAT). Other archaeal cells have walls made of polysaccharide, protein, or both.

The most common cell wall among archaeal species is a surface layer called the **S-layer**. It consists of hexagonal patterns of protein or glycoprotein that self-assemble into a crystalline lattice 5 nm to 25 nm thick.

Although the walls may be structurally different and the molecules form a different structural pattern, the function is the same as in bacterial species—to provide mechanical support and prevent osmotic lysis.

CONCEPT AND REASONING CHECKS

4.9 Distinguish between peptidoglycan and pseudopeptidoglycan cell walls.

Hydrophilic: Pertaining to molecules or parts of molecules that are soluble in water.

Hydrophobic: Pertaining to molecules or parts of molecules that are not soluble in water.

The Cell Membrane Represents the Interface between the Cell Environment and the Cell Cytoplasm

KEY CONCEPT

10. Molecules and ions cross the cell membrane by facilitated diffusion or active transport.

A **cell** (or **plasma**) **membrane** is a universal structure that separates external from internal (cytoplasmic) environments, preventing soluble materials from simply diffusing into and out of the cell. One exception is water, which due to its small size and overall lack of charge can diffuse slowly across the membrane.

The bacterial cell membrane, which is about 7 nm thick, is 40% phospholipid and 60% protein. In illustrations, the cell membrane appears very rigid (FIGURE 4.15). In reality, it is quite fluid, having the consistency of olive oil. This means the mosaic of phospholipids and proteins are not cemented in place, but rather they can move

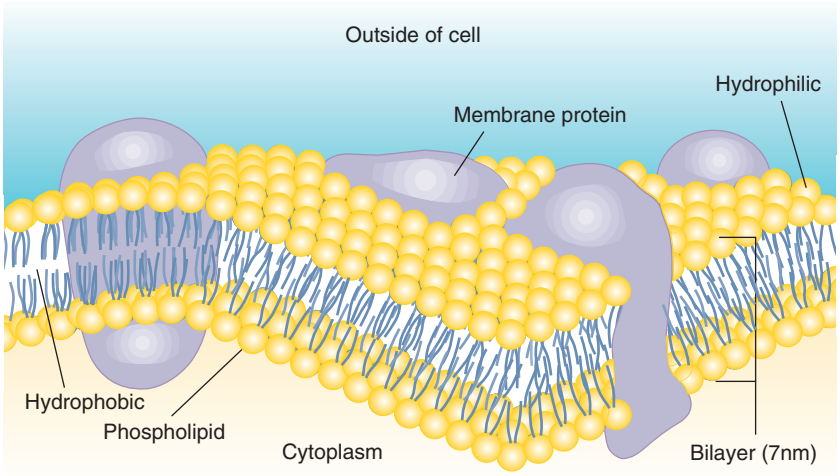


FIGURE 4.15 The Structure of the Bacterial Cell Membrane. The cell membrane of a bacterial cell consists of a phospholipid bilayer in which are embedded integral membrane proteins. Other proteins and ions may be associated with the integral proteins or the phospholipid heads. »» Why is the cell membrane referred to as a fluid mosaic structure?

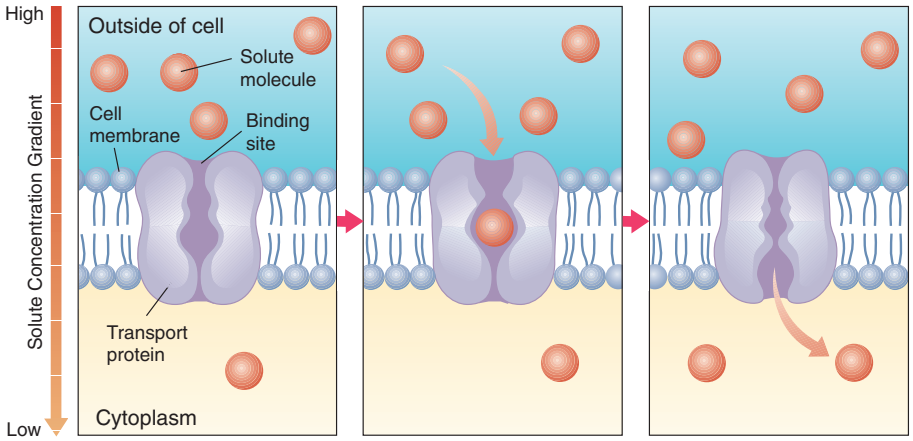


FIGURE 4.16 Facilitated Transport through a Membrane Protein. Many transport proteins facilitate the diffusion of nutrients across the lipid bilayer. The transport protein forms a hydrophilic channel through which a specific solute can diffuse. »» Why would a solute move through a membrane protein rather than simply across the lipid bilayer?

laterally in the membrane. This dynamic model of membrane structure therefore is called the **fluid mosaic model**.

The phospholipid molecules, typical of most biological membranes, are arranged in two parallel layers (a bilayer) and represent the barrier function of the membrane. The phospholipids contain a charged phosphate head group attached to two hydrophobic fatty acid chains (see Chapter 2). The fatty acid "tails" are the portion that forms the permeability barrier. In contrast, the hydrophilic head groups are exposed to the aqueous external or cytoplasmic environments.

Several antimicrobial substances act on the membrane bilayer. The antibiotic polymyxin pokes holes in the bilayer, while some detergents and alcohols dissolve the bilayer. Such action allows the cytoplasmic contents to leak out of bacterial cells, resulting in death through cell lysis.

A diverse population of membrane proteins populates the phospholipid bilayer. These membrane proteins often have stretches of hydrophobic amino acids that interact with the hydrophobic fatty acid chains in the membrane. These proteins span the width of the bilayer and are referred to as "integral membrane proteins". Other proteins, called "peripheral membrane proteins", are associated with the polar heads of the bilayer.

The membrane proteins carry out numerous important functions. Some represent enzymes needed for cell wall synthesis or for energy metabolism. As mentioned, bacterial and archaeal cells lack mitochondria and part of that organelle's function is carried out by the cell membrane. Other membrane proteins help anchor the DNA to the membrane during replication or act as receptors of chemical information, sensing changes in environment conditions and triggering appropriate responses.

Perhaps the largest group of integral membrane proteins is involved as transporters of charged solutes, such as amino acids, simple sugars, nitrogenous bases, and ions across the lipid bilayer. The transport systems are highly specific though, only transporting a single molecular species or a very similar class of molecules. Therefore, there are many different transport proteins to regulate the diverse molecular traffic that must flow into or out of a cell.

The transport process can be passive or active. In **facilitated diffusion**, integral membrane proteins facilitate the movement of materials down their concentration gradient; that is, from an area of higher concentration to one of lower concentration (FIGURE 4.16). By acting as a conduit for diffusion or as a transporter through the hydrophobic bilayer, hydrophilic solutes can enter or leave without the need for cellular energy.

Unlike facilitated diffusion, **active transport** allows different concentrations of solutes to be established outside or inside of the cell against the concentration gradient. These membrane proteins act as "pumps" and, as such, demand an energy input from the cell. Cellular processes such as cell energy production and flagella rotation also depend on active transport.

CONCEPT AND REASONING CHECKS

4.10 Justify the necessity for phospholipids and proteins in the cell membrane.

The Archaeal Cell Membrane Differs from Bacterial and Eukaryal Membranes

KEY CONCEPT

11. Archaeal membranes are structurally unique.

Besides the differences in gene sequences for ribosomal RNA in the domain *Archaea*, another major difference used to separate the archaeal organisms into their own domain is the chemical nature of the cell membrane.

The manner in which the hydrophobic lipid tails are attached to the glycerol is different in the *Archaea*. The tails are bound to the glycerol by "ether linkages" rather than the "ester linkages" found in the domains *Bacteria* and *Eukarya* (FIGURE 4.17A).

Also, typical fatty acid tails are absent from the membranes; instead, repeating five-carbon units are linked end-to-end to form lipid tails longer than the fatty acid tails. The result is a lipid **monolayer** rather than a bilayer (FIGURE 4.17B). This provides an advantage to the hyperthermophiles by preventing a peeling in two of the membrane, which would occur with a typical phospholipid bilayer structure.

CONCEPT AND REASONING CHECKS

4.11 What is unique about archaeal membrane structure?

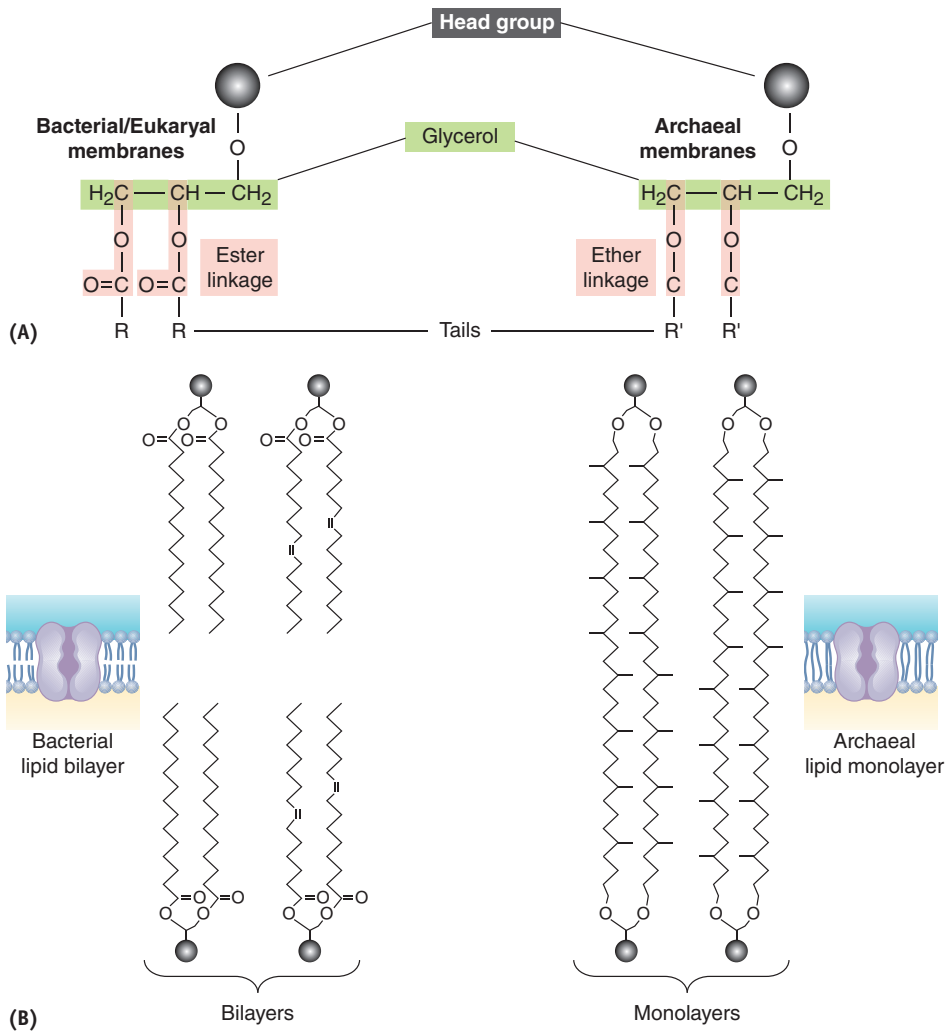


FIGURE 4.17 **Structure of Cell Membranes.** (**A**) Bacterial and eukaryal cell membranes involve an ester linkage joining the glycerol to the fatty acid tails (R) while archaeal membranes have an ether linkage to the isoprenoid tails (R'). (**B**) Bacterial and eukaryal membranes form a bilayer while archaeal membranes are a monolayer. »» What identifies an ester linkage from an ether linkage?

4.6 The Cell Cytoplasm and Internal Structures

The cell membrane encloses the **cytoplasm**, which is the compartment within which most growth and metabolism occur. The cytoplasm consists of the **cytosol**, a semifluid mass of proteins, amino acids, sugars, nucleotides, salts, vitamins, and ions—all dissolved in water (see Chapter 2)—and several bacterial structures or subcompartments, each with a specific function.

The Nucleoid Represents a Subcompartment Containing the Chromosome

KEY CONCEPT

12. The nucleoid contains the cell's essential genetic information.

The chromosome region in bacterial and archaeal cells appears as a diffuse mass termed the **nucleoid** (FIGURE 4.18). The nucleoid does not contain a covering or membrane; rather, it represents a central subcompartment in the cytoplasm where the DNA aggregates and ribosomes are absent. Usually there is a single chromosome per cell and, with few exceptions, exists as a closed loop of DNA and protein.

The DNA contains the essential hereditary information for cell growth, metabolism, and reproduction. Because most cells only have one chromosome, the cells are genetically haploid. Unlike eukaryotic microorganisms and other eukaryotes, the nucleoid and chromosome do not undergo mitosis and having but the one set of genetic information cannot undergo meiosis.

Haploid: Having a single set of genetic information.

The complete set of genes in an organism, called the **genome**, varies by species. For example, the genome of *E. coli*, a typical bacterial species in the mid-size range, contains about 4,300 genes. In all cases, these genes determine what proteins and enzymes the cell can make; that is, what metabolic reactions and activities can be carried out. For *E. coli*, this equates to some 2,000 different proteins. Extensive coverage of bacterial DNA is presented in Chapter 8.

CONCEPT AND REASONING CHECKS

4.12 Why do we say that the bacterial chromosome contains the "essential hereditary information"?

Plasmids Are Found in Many Bacterial and Archaeal Cells

KEY CONCEPT

13. Plasmids contain nonessential genetic information.

Besides a nucleoid, many bacterial and archaeal cells also contain smaller molecules of DNA called **plasmids**. About a tenth the size of the chromosome, these stable, extrachromosomal DNA molecules exist as closed loops containing 5 to 100 genes. There can be one or more plasmids in a cell and these may contain similar or different genes. Plasmids replicate independently of the chromosome and can be transferred between cells during recombination. They also represent important vectors in industrial technologies that use genetic engineering. Both topics are covered in Chapter 9.

Vectors: Genetic elements capable of incorporating and transferring genetic information.

Although plasmids may not be essential for cellular growth, they provide a level of genetic flexibility. For example, some plasmids possess genes for disease-causing toxins and many carry genes for chemical or antibiotic resistance. For this latter reason, these genetic elements often are called **R plasmids** (R for resistance).

CONCEPT AND REASONING CHECKS

4.13 What properties distinguish the bacterial chromosome from a plasmid?

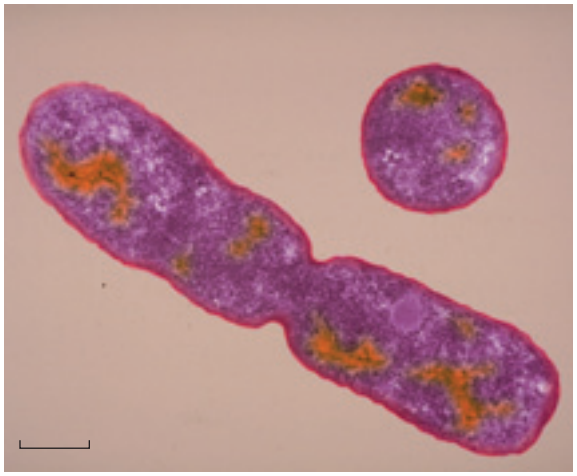


FIGURE 4.18 The Bacterial Nucleoid. In this false-color transmission electron micrograph of *Escherichia coli*, nucleoids (orange) occupy a large area in a bacterial cell. Both longitudinal (center cells) and cross sections (cell upper right) of *E. coli* are visable. (Bar = 0.5 µm.) »» How does a nucleoid differ from the eukaryotic cell nucleus described in the previous chapter?

Other Subcompartments Exist in the Cell Cytoplasm

KEY CONCEPT

14. Ribosomes, microcompartments, and inclusions carry out specific intracellular functions.

For a long time the cytoplasm was looked at as a bag enclosing the genetic machinery and biochemical reactions. As more studies were carried out with the electron microscope and with biochemical techniques, it became evident that the cytoplasm contained "more than meets the eye."

Ribosomes. One of the universal cell structures mentioned in Chapter 3 was the **ribosome**. There are hundreds of thousands of these nearly spherical particles in the cell cytoplasm, which gives it a granular appearance when viewed with the electron microscope (FIGURE 4.19A). Their relative size is measured by how fast they settle when spun in a centrifuge. Measured in Svedberg units (S), bacterial and archaeal ribosomes represent 70S particles.

The ribosomes are built from RNA and protein and are composed of a small subunit (30S) and a large subunit (50S) (FIGURE 4.19B). For proteins to be synthesized, the two subunits come together to form a 70S functional ribosome (Chapter 8). Some antibiotics, such as streptomycin and tetracycline, prevent bacterial and archaeal ribosomes from carrying out protein synthesis.

Microcompartments. Recently, some bacterial species have been discovered that contain **microcompartments**. The microcompartments appear to be unique to the *Bacteria* and consist of a polyprotein shell 100 to 200 nm in diameter (see Chapter 3). The shell surrounds various types of enzymes and, in the cyanobacteria, microcompartments called "carboxysomes" function to enhance carbon dioxide fixation. In some non-photosynthetic species, microcompartments limit diffusion of volatile or toxic metabolic products.

Inclusions. Cytoplasmic structures, called **inclusions**, can be found in the cytoplasm. Many of these bodies store nutrients or the monomers for cellular structures. For example, some inclusions consist of aggregates or granules of polysaccharides (glycogen), globules of elemental sulfur, or lipid. Other inclusion bodies can serve as important identification characters for bacterial pathogens. One example is the diphtheria bacilli that contain **metachromatic granules**, or **volutin**, which are deposits of polyphosphate (long chains of inorganic phosphate) along with calcium and other ions. These granules stain with dyes such as methylene blue.

Centrifuge: An instrument that spins particles suspended in liquid at high speed.

Some aquatic and marine forms float on the water surface, which is made possible by the presence of **gas vesicles**, cytoplasmic compartments built from a water-tight protein shell. These vesicles decrease the density of the cell, which generates and regulates their buoyancy.

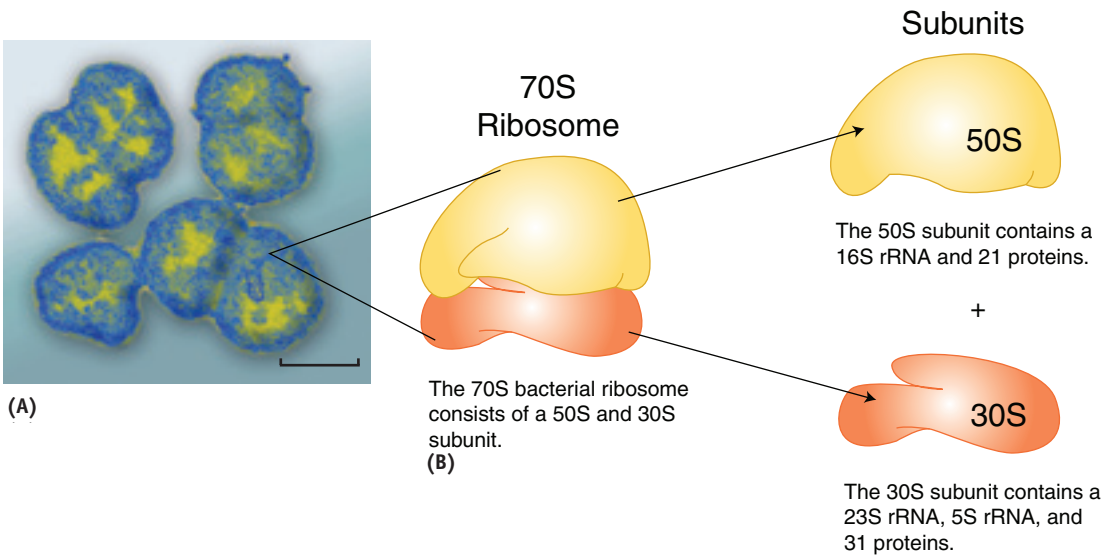


FIGURE 4.19 The Bacterial Ribosome. (**A**) A false-color electron microscope image of *Neisseria gonorrhoeae*, showing the nucleoid (yellow) and ribosomes (blue). (Bar = 1µm.) (**B**) The functional 70S ribosome is assembled from a small (30S) and large (50S) subunit. »» How many rRNA molecules and proteins construct a 70S ribosome?

The **magnetosome**, another type of inclusion or subcompartment, is described in MicroFocus 4.4. These bacterial inclusions are invaginations of the cell membrane, which are coordinated and positioned by cytoskeletal filaments similar to eukaryotic microfilaments.

CONCEPT AND REASONING CHECKS

4.14 Provide the roles for the subcompartments found in bacterial cells.

Many Bacterial/Archaeal Cells Have a "Cytoskeleton"

KEY CONCEPT

15. Cytoskeletal proteins regulate cell division and help determine cell shape.

Until recently, the dogma was that bacterial and archaeal cells lacked a cytoskeleton, which is a common feature in eukaryotic cells (see Chapter 3). However, it now appears cytoskeletal

MICROFOCUS 4.4: Environmental Microbiology

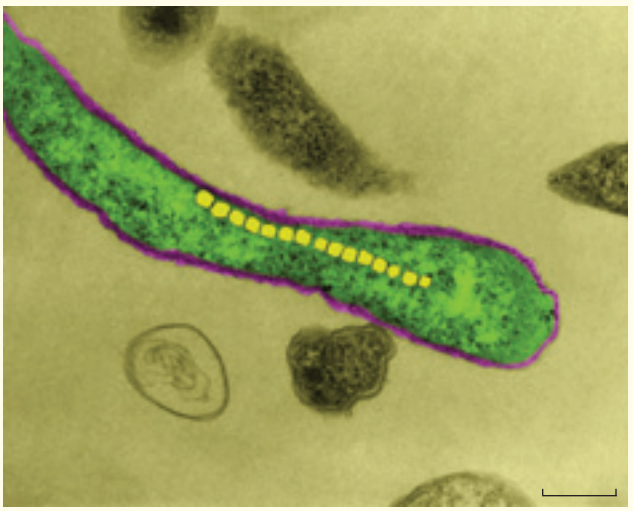
A "Not So Fatal" Attraction

To get from place to place, humans often require the assistance of maps, GPS systems, or gas station attendants. In the microbial world, life is generally more simple, and traveling is no exception.

In the early 1980s, Richard P. Blakemore and his colleagues at the University of New Hampshire observed mud-dwelling bacterial cells gathering at the north end of water droplets. On further study, they discovered each cell had a chain of aligned magnetic particles acting like a compass directing the organism's movements (magnetotaxis). Additional interdisciplinary investigations by microbiologists and physicists have shown the magnetotactic bacteria contain a linear array of 15–20 membrane-bound vesicles along the cell's long axis (see figure). Each vesicle, called a **magnetosome**, is an invagination of the cell membrane and contains the protein machinery to nucleate and grow a crystal of magnetite (Fe_3O_4) or greigite (Fe_3S_4). The chain of magnetosomes is organized by filaments that are similar to eukaryotic actin. By running parallel to the magnetosome chain, the filaments organize the vesicles into a chain. As each vesicle accumulates the magnetite or greigite crystal to form a magnetosome, magnetostatic interactions between vesicles stabilizes the linear aggregation.

To date, all magnetotactic bacterial cells are motile, gram-negative cells common in aquatic and marine habitats, including sediments where oxygen is absent. This last observation is particularly noteworthy because it explains why these organisms have magnetosomes.

It originally was thought that magnetotaxis was used to guide cells to those regions of the habitat with no oxygen; in other words, they travel downward toward the sediment. More recent studies have shown that some magnetotactic bacteria actually prefer low concentrations of oxygen. So the opinion now is that both magnetotaxis and aerotaxis work together to allow cells to "find" the optimal point within an oxygen gradient. This "not so fatal" attraction permits the bacteria to reach a sort of biological nirvana and settle in for a life of environmental bliss.



Bacterial magnetosomes (yellow) are seen in this false-color transmission electron micrograph of a magnetotactic marine spirillum. (Bar = 1 μm.)

proteins homologous to those in the eukaryotic cytoskeleton are present.

The first protein discovered was a homolog of the eukaryotic protein tubulin, which forms filaments that assemble into microtubules. The homolog forms filaments similar to those in microtubules but the filaments do not assemble into microtubules. These tubulin-like proteins have been found in all bacterial and archaeal cells examined and appear to function in the regulation of cell division. During this process, the protein localizes around the neck of the dividing cell where it recruits other proteins needed for the deposition of a new cell wall between the dividing cells (MicroFocus 4.5).

Protein homologs remarkably similar in three-dimensional structure to eukaryotic microfilaments assemble into filaments that help determine cell shape in *E. coli* and *Bacillus subtilis*. These homologs have been found in most non-spherical cells where they form a helical network beneath the cell membrane to guide the proteins involved in cell wall formation (FIGURE 4.20A). The homologs also are involved with chromosome segregation during cell division and magnetosome formation.

Homolog:
An entity with similar attributes due to shared ancestry.

Intermediate filaments (IF), another component of the eukaryotic cytoskeleton in some metazoans, have a homolog as well. The protein, called crescentin, helps determine the characteristic crescent shape of *Caulobacter crescentus* cells.

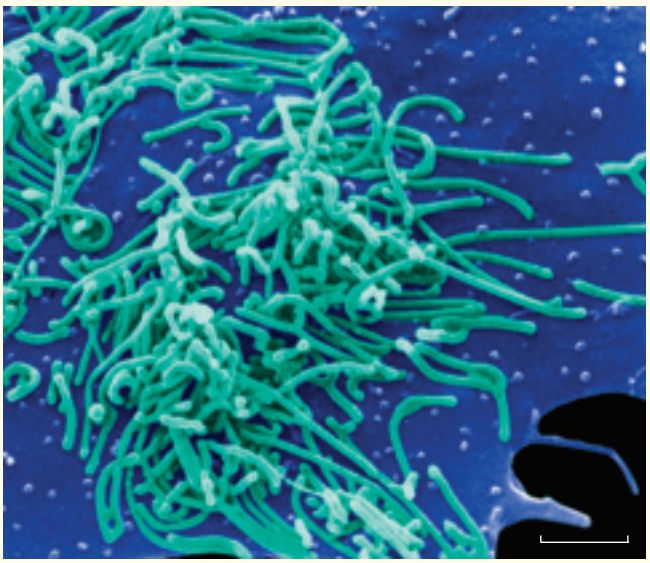
Metazoans:
Members of the vertebrates, nematodes, and mollusks.

MICROFOCUS 4.5: Public Health
The Wall-less Cytoskeleton

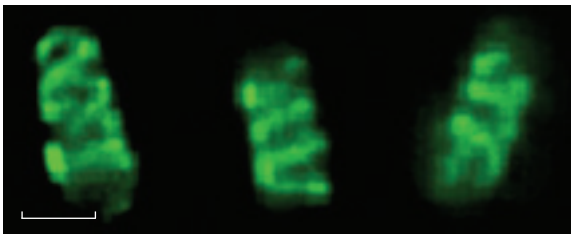
Sometimes the lack of something can speak loudly. Take for example the mycoplasmas such as *Mycoplasma pneumoniae* that causes primary atypical pneumonia (walking pneumonia). This, as well as other *Mycoplasma* species, lack a cell wall. How then can they maintain a defined cell shape (see figure)?

Transmission electron microscopy has revealed that mycoplasmal cells contain a very complex cytoskeleton and further investigations indicate the cytoskeletal proteins are very different from the typical cytoskeletal homologs found in other groups of the Firmicutes. For example, *Spiroplasma citri,* which causes infections in other animals, has a fibril protein cytoskeleton that is laid down as a helical ribbon. This fibril protein has not been found in any other organisms. Because the cells are spiral shaped, the ribbon probably is laid down in such a way to determine cell shape, suggesting that shape does not have to be totally dependent on a cell wall.

In *Mycoplasma genitalium,* which is closely related to *M. pneumoniae* and causes human urethral infections, a eukaryotic-like tubulin homolog has been identified, but none of the other proteins have been identified that it recruits at the division neck for cell division. Surprising? Not really. Important? Immensely! Because mycoplasmas do not have a cell wall, why would they require those proteins that lay down a peptidoglycan cross wall between cells? So the lack of something (wall-forming proteins) tells us what those proteins must do in their gram-positive relatives that do have walls.



False-color scanning electron micrograph of *Mycoplasma pneumoniae* cells. (Bar = 2.5 µm.)



(A)

(B)

FIGURE 4.20 A Bacterial Cytoskeleton. Bacterial cells have proteins similar to those that form the eukaryotic cytoskeleton. (**A**) Microfilament-like proteins form helical filaments that curve around the edges of these cells of *Bacillus subtilis*. (Bar = 1.5 µm.) (**B**) Three-dimensional model of a helical *Caulobacter crescentus* cell (green) with a helical cytoskeletal filament of crescentin (pink).
»» What would be the shape of these cells without the cytoskeletal proteins?

In older cells that become filamentous, crescentin maintains the helical shape of the cells by aligning with the inner cell curvature beneath the cytoplasmic membrane (FIGURE 4.20B).

Even though the evolutionary relationships are quite distant between bacterial/archaeal and eukaryotic cytoskeletal proteins based on protein sequence data, the similarity of their three-dimensional structure and function is strong evidence supporting homologous cytoskeletons.

CONCEPT AND REASONING CHECKS

4.15 Evaluate the relationship between the eukaryotic cytoskeleton and the cytoskeletal protein homologs in bacterial and archaeal cells.

4.7 The Bacteria/Eukaryote Paradigm—Revisited

TABLE 4.3 summarizes the structural features of bacterial and archaeal cells. One of the take-home lessons from the table, and discussions of cell structure and function explored in this chapter (and the initial discussion of the bacteria/eukaryote paradigm in Chapter 3), is the ability of these organisms to carry out the "complex" metabolic and biochemical processes typically associated with eukaryotic cells—usually without the need for elaborate membrane-enclosed subcompartments.

What Is a Prokaryote?

KEY CONCEPT

16. Cellular processes in bacterial cells can be similar to those in eukaryotic cells.

Earlier in this chapter, the intricate subcellular compartmentation was discussed for several cell structures. What about other major cellular processes such as making proteins? This requires two processes, that of transcription and translation (Chapter 8). In eukaryotic cells, these processes are spatially separated into the cell nucleus (transcription) and the cytoplasm (translation).

In bacterial and archaeal cells, there also can be spatial separation between transcription and translation FIGURE 4.21. The RNA polymerase molecules needed for transcription are localized to a region separate from the ribosomes and other proteins that perform translation. So, even without a nuclear membrane, these cells can separate the process involved in

TABLE

4.3 A Summary of the Structural Features of Bacterial and Archaeal Cells

Structure	Chemical Composition	Function	Comment
External Structures			
Pili	Protein	Attachment to surfaces Genetic transfer	Found primarily in gram-negative bacteria
Flagella	Protein	Motility	Present in many rods and spirilla; few cocci; vary in number and placement
Glycocalyx	Polysaccharides and small proteins	Buffer to environment Attachment to surfaces	Capsule and slime layer Contributes to disease development Found in plaque bacteria and biofilms
Cell Envelope			
Cell wall		Cell protection Shape determination Cell lysis prevention	
Bacterial	Gram positives: thick peptidoglycan and teichoic acid		Site of activity of penicillin and lysozyme
	Gram negatives: little peptidoglycan and an outer membrane		Gram-negative bacteria release endotoxins
Archaeal	Pseudopeptidoglycan Protein		S-layer
Cell membrane			
Bacterial Archaeal	Protein and phospholipid	Cell boundary Transport into/out of cell Site of enzymatic reactions	Lipid bilayer Lipid monolayer
Internal Structures			
Nucleoid	DNA	Site of essential genes	Exists as single, closed loop chromosome
Plasmids	DNA	Site of nonessential genes	R plasmids
Ribosomes	RNA and protein	Protein synthesis	Inhibited by certain antibiotics
Microcompartments	Various metabolic enzymes	Carbon dioxide fixation Retention of volatile or toxic metabolites	Enzymes are enclosed in a protein shell
Inclusions	Glycogen, sulfur, lipid	Nutrient storage	Used as nutrients during starvation periods
Metachromatic granules	Polyphosphate	Storage of polyphosphate and calcium ions	Found in diphtheria bacilli
Gas vesicles	Protein shells	Buoyancy	Helps cells float
Magnetosome habitat	Magnetite/greigite	Cell orientation	Helps locate preferred
Cytoskeleton	Proteins	Cell division, chromosomal segregation, cell shape	Functionally similar to eukaryotic cytoskeletal proteins

MICROINQUIRY 4
The Prokaryote/Eukaryote Model

"It is now clear that among organisms there are two different organizational patterns of cells, which Chatton . . . called, with singular prescience, the eukaryotic and prokaryotic type. The distinctive property of bacteria and blue-green algae is the prokaryotic nature of their cells. It is on this basis that they can be clearly segregated from all other protists (namely, other algae, protozoa and fungi), which have eukaryotic cells."

Stanier and van Niel (1962)
—*The concept of a bacterium.*

The idea of a tree of life extends back centuries and originates not with scientific thinking, but rather with folklore and culture, and often focused on immortality or fertility (see figure).

The development of the three-domain tree of life, on the other hand, represents the evolutionary relationships between species. Its development has made a profound change in biology. Instead of two kinds of organisms—prokaryotes and eukaryotes—there are three: *Bacteria, Archaea,* and *Eukarya*.

Glass mosaic of tree of life on a wall of the 16th century Sim Wat Xiang Thong Luang Prabang UNESCO World Heritage Site, Laos.

In 2006, Norm Pace, a molecular biologist turned evolutionist at the University of Colorado, Boulder, suggested that the massive data bank of gene sequences identified since 1995 shows just how different archaeal organisms are from bacterial organisms and, in some ways, the archaeal ones are more similar to eukaryotic organisms. Therefore, Pace says, "we need to reassess our understanding of the course of evolution at the most fundamental level." Among items needing reassessment is the prokaryotic/eukaryotic paradigm—the tradition (folklore) if you will—that if an organism is not a eukaryote, it must be a prokaryote.

The quote at the top of the page refers to Edouard Chatton who coined the terms "prokaryotic" and "eukaryotic." Interestingly, neither he, nor Stanier and van Niel, ever really made mention as to

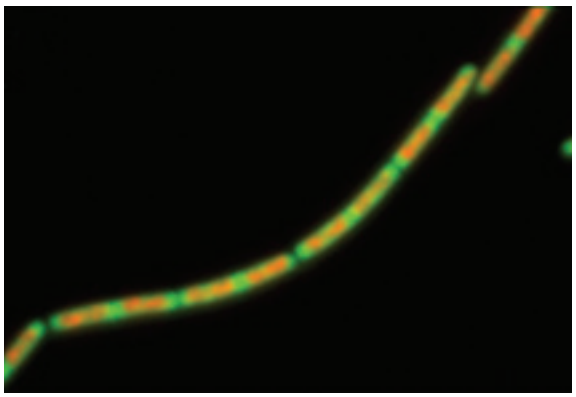


FIGURE 4.21 Spatial Separation of Transcription and Translation. In these cells of *Bacillus subtilis*, fluorescence microscopy was used to identify RNA polymerase (transcription) using a red fluorescent protein and ribosomes (translation) using a green fluorescent protein. Separate subcompartments are evident. (Bar = 3 µm.)
»» What does the spatial separation indicate concerning compartmentation?

making cellular proteins, in a manner similar to eukaryotic cells.

Traditionally, a prokaryote was an organism without a cell nucleus; that is, without a membrane surrounding the DNA or chromosome. But is that a fair way to describe all bacterial and archaeal organisms? In this chapter, you have learned that there are many basic differences between bacterial and archaeal cells, yet do we lump them together just because they both lack a cell nucleus? Some scientists say no—the terms "prokaryote" and "prokaryotic" are not appropriate for these two domains of life.

So, to finish this chapter, take a look at MICROINQUIRY 4, which discusses the prokaryotic/eukaryotic model for living organisms.

CONCEPT AND REASONING CHECKS

4.16 Make a list of the various subcompartments in bacterial cells.

what a prokaryotic cell is. Yet if you look in any introductory biology textbook, prokaryote is defined as a group of organisms that lack a cell nucleus. According to Pace, "the prokaryote/eukaryote model for biological diversity and evolution is invalid." How can all organisms without a cell nucleus be called "prokaryotic," especially because the eukaryotic cell nucleus appears to be descended from as ancient a line of cells as the *Archaea?* Yes, the concept of a nuclear membrane (or not) is important, but no more important than other cellular properties. And the problem is that the word "prokaryote" is so engrained in the culture of biology and in the scientific mind of biologists—and students—that inappropriate inferences about organisms are made using this term. Pace does not buy the argument that the term "prokaryote" can be used to identify organisms that are not eukaryotes because the *Bacteria* are very different from the *Archaea* and, therefore, should not be put under the umbrella of "prokaryote."

Pace believes saying that prokaryotes lack a cell nucleus is a scientifically invalid description; although open to debate, he says no one can define what a prokaryote is—only what it is not (e.g., no nucleus, no mitochondria, no chloroplasts, no endomembrane system, etc.). Therefore, lumping the *Bacteria* and *Archaea* conceptually dismisses the fundamental and important differences between these two kinds of organisms and reinforces an incorrect understanding of biological organization and evolution.

Pace believes it is time to delete the term prokaryote as a term for bacterial and archaeal organisms. Because it has long been used by all biology texts, including this one (although in many cases "bacteria" and "archaea" have replaced the term prokaryote), Pace says he realizes "it is hard to stop using the word, prokaryote."

Discussion Point

There is no doubt that bacterial and archaeal organisms are very different entities. So, if "prokaryote" is to be deleted from the biological vocabulary, what can we call the Bacteria *and* Archaea*? Can you think of some positive characters that would define both bacterial and archaeal cells? If so, then how about inventing a common noun and adjective for both? Or do we simply speak of the bacteria, archaea, and eukaryotes separately?*

SUMMARY OF KEY CONCEPTS

4.1 Diversity among the *Bacteria* and *Archaea*

1. The **phylogenetic tree** of life contains many bacterial phyla and groups, including the **Proteobacteria**, **Gram-positive bacteria**, **Cyanobacteria**, **Chlamydiae**, and **Spirochaetes**.
2. Many organisms in the domain *Archaea* live in extreme environments. The **Euryarchaeota** (methanogens, extreme halophiles, and the thermoacidophiles) and the **Crenarchaeota** are the two phyla.

4.2 Cell Shapes and Arrangements

3. **Bacilli** have a cylindrical shape and can remain as single cells or be arranged into **diplobacilli** or chains (**streptobacilli**). **Cocci** are spherical and form a variety of arrangements, including the **diplococcus**, **streptococcus**, and **staphylococcus**. The spiral-shaped bacteria can be curved rods (**vibrios**) or spirals (**spirochetes** and **spirilla**). Spirals generally appear as single cells.

4.3 An Overview to Bacterial and Archaeal Cell Structure

4. Cell organization is centered on three specific processes: sensing and responding to environmental changes, compartmentalizing metabolism, and growing and reproducing.

4.4 External Cell Structures

5. **Pili** are short hair-like appendages found on many gram-negative bacteria to facilitate attachment to a surface. **Conjugation pili** are used for genetic transfer of DNA.
6. One or more **flagella**, found on many rods and spirals, provide for cell motility. Each flagellum consists of a **basal body** attached to the flagellar filament. In nature, flagella propel bacterial cells toward nutrient sources (**chemotaxis**). Spirochetes have **endoflagella**, while other bacterial species undergo gliding motility.
7. The **glycocalyx** is a sticky layer of polysaccharides that protects the cell against desiccation, attaches it to surfaces, and helps evade immune cell attack. The glycocalyx can be thick and tightly bound to the cell (**capsule**) or thinner and loosely bound (**slime layer**).

4.5 The Cell Envelope

8. The **cell wall** provides structure and protects against cell lysis. Gram-positive bacteria have a thick wall of **peptidoglycan** strengthened with **teichoic acids**. Gram-negative cells have a single layer of peptidoglycan and an **outer membrane** containing **lipopolysaccharide** and **porin proteins**.

9. Archaeal cell walls lack peptidoglycan but may have either a **pseudopeptidoglycan** or **S-layer**.
10. The **cell membrane** represents a permeability barrier and the site of transfer for nutrients and metabolites into and out of the cell. The cell membrane reflects the **fluid mosaic model** for membrane structure in that the lipids are fluid and the proteins are a mosaic that can move laterally in the bilayer.
11. The archaeal cell membrane links lipids through an ether linkage and the lipid tails are bonded together into a single **monolayer**.

4.6 The Cell Cytoplasm and Internal Structures

12. The DNA (**bacterial chromosome**), located in the **nucleoid**, is the essential genetic information and represents the organism's **genome**.
13. Bacterial and archaeal cells may contain one or more **plasmids**, circular pieces of nonessential DNA that replicate independently of the chromosome.
14. **Ribosomes** carry out protein synthesis, **microcompartments** carry out species-specific processes, while inclusions store nutrients or structural building blocks.
15. The **cytoskeleton**, containing protein homologs to the cytoskeletal proteins in eukaryotic cells, helps determine cell shape, regulates cell division, and controls chromosomal segregation during cell division.

4.7 The Bacteria/Eukaryote Paradigm—Revisited

16. Cell biology investigations are showing that compartmentation in bacterial cells can occur; it simply does not require the diverse membranous organelles typical of eukaryotic cells.

LEARNING OBJECTIVES

After understanding the textbook reading, you should be capable of writing a paragraph that includes the appropriate terms and pertinent information to answer the objective.

1. Identify the major bacterial phyla described in this chapter and provide characteristics for each group.
2. Explain why many archaeal organisms are considered **extremophiles**.
3. Compare the various shapes and arrangements of bacterial and archaeal cells.
4. Summarize how the processes of sensing and responding to the environment, compartmentation of metabolism, and growth and metabolism are linked to cell structure.
5. Assess the role of **pili** to bacterial colonization and infection.
6. Describe the structure of bacterial flagella and discuss how they function in **chemotaxis**.
7. Differentiate between a **capsule** and **slime layer**. Identify their roles in cell survival.
8. Compare and contrast the structure of a **gram-positive cell wall** with a **gram-negative cell wall**.
9. Summarize the differences between bacterial and archaeal cell walls.
10. Justify the need for a **cell membrane** surrounding all bacterial and archaeal cells.
11. Explain how the structure of archaeal cell membranes differs from bacterial cell membranes.
12. Describe the structure of the **nucleoid**.
13. Judge the usefulness of **plasmids** to cell metabolism and organismal survival.
14. List the typical **inclusions** found in the bacterial cell cytoplasm and identify their contents or roles.
15. Describe three roles that the bacterial **cytoskeleton** plays.
16. Justify the statement, "Bacterial cells are as highly organized subcellularly as are eukaryotic cells."

STEP A: SELF-TEST

Each of the following questions is designed to assess your ability to remember or recall factual or conceptual knowledge related to this chapter. Read each question carefully, then select the ***one*** answer that best fits the question or statement. Answers to even-numbered questions can be found in **Appendix C**.

1. Which one of the following is NOT a genus within the gram-positive bacteria?
   A. *Staphylococcus*
   B. Methanogens
   C. *Mycoplasma*
   D. *Bacillus* and *Clostridium*
2. The domain *Archaea* includes all the following groups *except* the
   A. mycoplasmas.
   B. extreme halophiles.
   C. Crenarchaeota.
   D. Euryarchaeota.
3. Spherical bacterial cells in chains would be a referred to as a _____ arrangement.
   A. vibrio
   B. streptococcus
   C. staphylococcus
   D. tetrad
4. Intracellular organization in bacterial and archaeal species is centered around
   A. compartmentation of metabolism.
   B. growth and reproduction.
   C. sensing and responding to environment.
   D. All the above (**A–C**) are correct.

5. Which one of the following statements does NOT apply to pili?
   A. Pili are made of protein.
   B. Pili allow for attachment to surfaces.
   C. Pili facilitate nutrient transport.
   D. Pili contain adhesins.
6. Flagella are
   A. made of carbohydrate and lipid.
   B. found on all bacterial cells.
   C. shorter than pili.
   D. important for chemotaxis.
7. Capsules are similar to pili because both
   A. contain DNA.
   B. are made of protein.
   C. contain dextran fibers.
   D. permit attachment to surfaces.
8. Gram-negative bacteria would stain _____ with the Gram stain and have _____ in the wall.
   A. orange-red; teichoic acid
   B. orange-red; lipopolysaccharide
   C. purple; peptidoglycan
   D. purple; teichoic acid
9. The cell membrane of archaeal cells contains
   A. a monolayer.
   B. sterols.
   C. ester linkages.
   D. All the above (**A**–**C**) are correct.
10. The movement of glucose into a cell occurs by
    A. facilitated diffusion.
    B. active transport.
    C. simple diffusion.
    D. phospholipid exchange.
11. When comparing bacterial and archaeal cell membranes, only bacterial cell membranes
    A. have three layers of phospholipids.
    B. have a phospholipid bilayer.
    C. are fluid.
    D. have ether linkages.
12. Which one of the following statements about the nucleoid is NOT true?
    A. It contains a DNA chromosome.
    B. It represents a nonmembranous subcompartment.
    C. It represents an area devoid of ribosomes.
    D. It contains nonessential genetic information.
13. Plasmids
    A. replicate with the bacterial chromosome.
    B. contain essential growth information.
    C. may contain antibiotic resistance genes.
    D. are as large as the bacterial chromosome.
14. Which one of the following is NOT a structure or subcompartment found in bacterial cells?
    A. Microcompartments
    B. Volutin
    C. Ribosomes
    D. Mitochondria
15. The bacterial cytoskeleton
    A. transports vesicles.
    B. helps determine cell shape.
    C. is organized identical to its eukaryotic counterpart.
    D. centers the nucleoid.
16. The bacterial cell is capable of
    A. spatial separation of metabolic processes.
    B. carrying out complex metabolic processes.
    C. subcompartmentalizing biochemical processes.
    D. All the above (**A**–**C**) are correct.

STEP B: REVIEW

Answers to even-numbered questions or statements can be found in **Appendix C**.

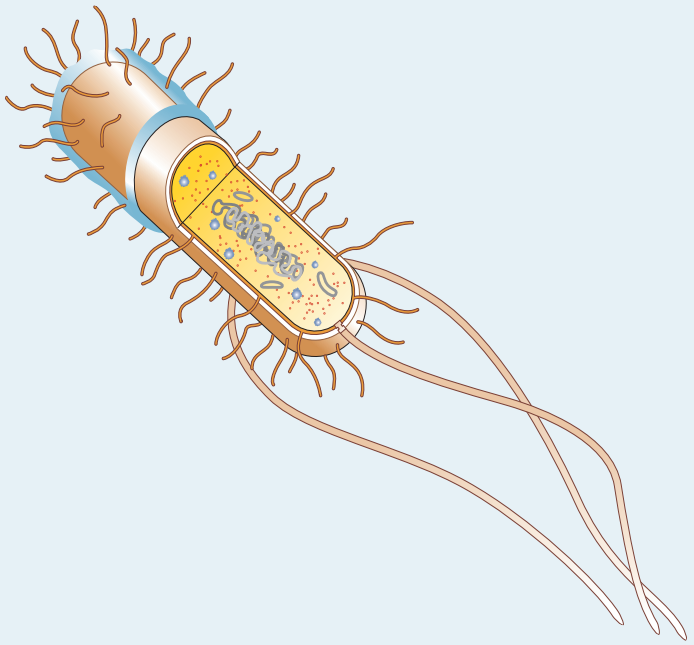
17. Construct a concept map for the **domain *Bacteria*** using the following terms.

Actinobacteria	hyperthermophiles
Bacillus	*Mycoplasma*
blooms	Proteobacteria
Chlamydiae	rickettsiae
Cyanobacteria	Spirochaetes
Escherichia	*Staphylococcus*
Firmicutes	*Streptomyces*
gram-negative species	*Treponema*
gram-positive species	

18. Construct a concept map for the **Cell Envelope** using the following terms.

active transport	membrane proteins
cell membrane	NAG
cell wall	NAM
endotoxin	outer membrane
facilitated transport	peptidoglycan
fluid-mosaic model	periplasm
gram-negative wall	phospholipids
gram-positive wall	polysaccharide
lipid A	porin proteins
lipopolysaccharide (LPS)	teichoic acid

Identify and label the structure on the accompanying bacterial cell from each of the following descriptions. Some separate descriptions may apply to the same structure.



Descriptions

19. An essential structure for chemotaxis, aerotaxis, or phototaxis.
20. Contains nonessential genetic information that provides genetic variability.
21. The structure that synthesizes proteins.
22. The protein structures used for attachment to surfaces.
23. Contains essential genes for metabolism and growth.
24. Prevents cell desiccation.
25. A 70S particle.
26. Contains peptidoglycan.
27. Regulates the passage of substances into and out of the cell.
28. Extrachromosomal loops of DNA.
29. Represents a capsule or slime layer.
30. The semifluid mass of proteins, amino acids, sugars, salts, and ions dissolved in water.

STEP C: APPLICATIONS

Answers to even-numbered questions can be found in **Appendix C**.

31. A bacterium has been isolated from a patient and identified as a gram-positive rod. Knowing that it is a human pathogen, what structures would it most likely have? Explain your reasons for each choice.
32. Another patient has a blood infection caused by a gram-negative bacterium. Why might it be dangerous to prescribe an antibiotic to treat the infection?
33. In the research lab, the gene for the cytoskeletal protein similar to eukaryotic tubulin is transferred into the DNA chromosome of a coccus-shaped bacterium. When this cell undergoes cell division, predict what shape the daughter cells will exhibit. Explain your answer.

STEP D: QUESTIONS FOR THOUGHT AND DISCUSSION

Answers to even-numbered questions can be found in **Appendix C**.

34. In reading a story about a bacterium that causes a human disease, the word "bacillus" is used. How would you know if the article is referring to a bacterial shape or a bacterial genus?
35. Suppose this chapter on the structure of bacterial and archaeal cells had been written in 1940, before the electron microscope became available. Which parts of the chapter would probably be missing?
36. Why has it taken so long for microbiologists to discover microcompartments and a cytoskeleton in bacterial and archaeal cells?
37. Apply the current understanding of the bacteria/eukaryote paradigm to the following statement: "Studying the diversity of life only accentuates life's unity."

HTTP://MICROBIOLOGY.JBPUB.COM/

The site features eLearning, an online review area that provides quizzes and other tools to help you study for your class. You can also follow useful links for in-depth information, read more MicroFocus stories, or just find out the latest microbiology news.