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.


"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 domain Bacteria...
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.

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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.
4.1 Diversity among the Bacteria and Archaea

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 Rocky Mountain spotted fever.
MICROFOCUS 4.1

Bacteria in Eight Easy Lessons

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.

Amazing: 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.

Along 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.
4.1 Diversity among the *Bacteria* and *Archaea*

**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 4.3D). 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 4.3E). 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.

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 Chlamydiaceae 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 Spirochaetaceae 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 reproductive 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.

**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 archaean genera that thrive under more modest conditions. The archaean 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 (*methan* = “methane”; *gen* = “produce”) are killed by oxygen gas and therefore are found in environments devoid of oxygen gas. The pro-

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**Additional Notes:**

- **Blooms:** Sudden increases in the numbers of cells of an organism in an environment.
- **FIGURE 4.3C, FIGURE 4.3E, FIGURE 4.3D:** Visual representations or illustrations related to the content of the text.
- **KEY CONCEPT:** Highlighted sections for key learning points.
- **Concept and Reasoning Checks:** Questions for readers to consider and respond to.
- **Archaea Classification:** Details on the classification and characteristics of archaea, including their ability to thrive in extreme environments.
4.1 Diversity among the Bacteria and Archaea

Crenarchaeota. The second phylum, the Crenarchaeota, are mostly hyperthermophiles growing at temperatures above 80°C. Hot sulfur springs are one environment where these archaean 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.

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.

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

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 archaean species grow, why have others adapted to such extreme environments?
### TABLE 4.1

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

### 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). 

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-
4.2 Cell Shapes and Arrangements

4.2.1 Cell Shapes and Arrangements

Four common shapes of bacterial cells are bacillus, coccus, spiral, and vibrio. Bacillus (rod) can be used to describe cell shape and arrangement, or a bacterial genus (Streptobacillus and Staphylococci).

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, is 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.

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**

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...
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?

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### 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.

#### 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; *plius* = “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”).

**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**

**What would happen if pili lacked adhesins?**
4.4 External Cell Structures

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.

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.

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. 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.

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FIGURE 4.9  Bacterial Flagella. (A) A light micrograph of <i>Proteus vulgaris</i> 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”?**

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...
4.4 External Cell Structures

- **Outer membrane**
- **Cell membrane**
- **Peptidoglycan layer**
- **Endoflagella**

Endoflagella lie between the peptidoglycan and the outer membrane. This spirochete has a single endoflagellum at each pole. Endoflagella from the two poles overlap for much of the cell length.

**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.

**Predict the behavior of a bacterial cell if it sensed a repellent; that is a potential harmful or lethal chemical.**

- **Chemotaxis**: A behavioral response to chemicals. 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. 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.

**FIGURE 4.10** Chemotaxis. (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 repellent; that is a potential harmful or lethal chemical.**

- **Glycocalyx**: 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 phagocytic surface.
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.
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**

- 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.

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

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**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?

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.
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).
4.5 The Cell Envelope

- **A** Structure of peptidoglycan

- **B** Gram-positive cell wall

- **C** Gram-negative cell wall

**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.
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.

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.

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

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

**The Archael Cell Wall Also Provides Mechanical Strength**

**KEY CONCEPT**

9. Archael cell walls have crystalline layers.

Archaal 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 archael cells have walls made of polysaccharide, protein, or both.

**TABLE 4.2**

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Gram Positive</th>
<th>Gram Negative</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peptidoglycan</td>
<td>Yes, thick layer</td>
<td>Yes, thin layer</td>
</tr>
<tr>
<td>Teichoic acids</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Outer membrane</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Lipopolysaccharides (LPS)</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Porin proteins</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Periplasm</td>
<td>No</td>
<td>Yes</td>
</tr>
</tbody>
</table>

**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 4.13). 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...
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.

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

The fluid mosaic model is a dynamic model of membrane structure. It is based on the idea that the phospholipid bilayer is the main structural component of the cell membrane. The hydrophilic heads of the phospholipids are exposed to the external or cytoplasmic environments, while the hydrophobic tails form the permeability barrier. The integral membrane proteins are embedded in the lipid bilayer, and they interact with the hydrophilic heads of the phospholipids.

The membrane proteins carry out a variety of functions, including transport, energy metabolism, and regulation of cell functions. They can be classified into two types: integral membrane proteins, which are embedded in the lipid bilayer, and peripheral membrane proteins, which are associated with the polar heads of the bilayer.

Facilitated diffusion is the process by which integral membrane proteins transport substances across the lipid bilayer. These proteins form a hydrophilic channel through which specific solutes can diffuse. Unlike passive transport, facilitated diffusion can move substances against a concentration gradient, but it requires energy input from the cell.

Active transport is a process by which integral membrane proteins pump substances across the lipid bilayer against their concentration gradients. These proteins act as “pumps” and demand energy input from the cell. Cellular processes such as cell energy production and flagella rotation also depend on active transport.
The Archaeal Cell Membrane Differs from Bacterial and Eukaryal Membranes

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.

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 the one set of genetic information cannot undergo meiosis.

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.

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?
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.

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.

The 70S bacterial ribosome consists of a 50S and 30S subunit. (B) The 50S subunit contains a 16S rRNA and 21 proteins. The 30S subunit contains a 23S rRNA, 5S rRNA, and 31 proteins.
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...

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.

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 (Fe₃O₄) or greigite (Fe₃S₄). 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).

**MicroFocus 4.5: Public Health**

<table>
<thead>
<tr>
<th>The Wall-less Cytoskeleton</th>
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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, an 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.)
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...
### 4.7 The Bacteria/Eukaryote Paradigm—Revisited

#### Table 4.3: A Summary of the Structural Features of Bacterial and Archaeal Cells

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

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### 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 thermocacidophiles) 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). Coccii are spherical and form a variety of arrangements, including the diplococci, streptococci, and staphylococci. 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 teicholic acids. Gram-negative cells have a single layer of peptidoglycan and an outer membrane containing lipopolysaccharide and porin proteins.
4.6 The Cell Cytoplasm and Internal Structures

9. Archael 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 archael cell membrane links lipids through an ether linkage and the lipid tails are bonded together into a single monolayer.

12. The DNA (bacterial chromosome), located in the nucleoid, is the essential genetic information and represents the organism's genome.

13. Bacterial and archael 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 archael organisms are considered extremophiles.
3. Compare the various shapes and arrangements of bacterial and archael 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 archael cell walls.
10. Justify the need for a cell membrane surrounding all bacterial and archael cells.
11. Explain how the structure of archael 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. Eurarchaeota.
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 archael 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.

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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 archaean 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.

17. Construct a concept map for the domain Bacteria using the following terms.
    Actinobacteria
    Bacillus
    blooms
    Chlamydiae
    Cyanobacteria
    Escherichia
    Firmicutes
    gram-negative species
    gram-positive species
    hyperthermophiles
    Mycoplasma
    Proteobacteria
    rickettsiae
    Spirochaetes
    Staphylococcus
    Streptomyces
    Treponema

18. Construct a concept map for the Cell Envelope using the following terms.
    active transport
    membrane proteins
    cell membrane
    NAG
    NAM
    cell wall
    endotoxin
    outer membrane
    peptidoglycan
    facilitated transport
    periplasm
    fluid-mosaic model
    phospholipids
    gram-negative wall
    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.
24. Prevents cell desiccation.
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.”

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