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CHAPTER

2 Microbial Cell Structure and Function

Summary

Chapter 2 is an excellent introductory overview of the structure and function of both prokaryotic and eukaryotic cells. For courses designed for nonscience majors, this chapter provides general details on each topic that, if supplemented with material from related chapters later in the text, may be sufficient background for most students. However, it is recommended that Chapter 2 be used to set the stage for more detailed coverage later in the course.

2.1–2.5 | The Cell Envelope

Introduce this chapter by giving the definition of cell envelope and its function. Then focus your discussion on the major components of the cell envelope including the cytoplasmic membrane (Section 2.1). The structure of the cytoplasmic membrane, a phospholipid bilayer, should be discussed in considerable detail because it plays a critical role in establishing and maintaining the cell's internal environment. Students must understand that the cytoplasmic membrane is the *selectively permeable* boundary between the cytoplasm of the cell and the cell's immediate environment. If the integrity of the membrane becomes compromised, then essential cellular components can leak out of the cytoplasm and into the environment, thereby destroying the cell. Convey to students that the cytoplasmic membrane generally does *not* confer a specific shape and provide rigid support to the cell (these are roles of the cell wall, to be discussed later), but rather the membrane has a fluid nature that allows for a degree of lateral movement of phospholipids and proteins (Figures 2.1 and 2.2). Proteins embedded in the membrane consist of both hydrophobic regions that are situated within the lipid portion of the phospholipid bilayer and hydrophilic regions that are oriented toward either the external environment or the aqueous cytoplasm of the cell.

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While members of the *Bacteria* and *Eukarya* contain *ester* linkages that bond the fatty acids to glycerol in their membranes (Figure 2.1), *Archaea* contain *ether* linkages between the glycerol and lipid portions of their membranes (Figure 2.3). In addition, archaeal membrane lipids are not composed of fatty acids but instead consist of repeating five-carbon *isoprene* units (compare Figures 2.1 and 2.3) that combine to form 20-carbon *phytanyl* side chains (Figure 2.3). Together, the glycerol and phytanyl form a *glycerol diether*. In some *Archaea*, glycerol diethers are joined at their hydrophobic ends to create a *lipid monolayer* of diglycerol tetraethers (Figure 2.3*b* and *c*). Archaeal lipids can have various isoprenoid chains that contain ring structures. For example, members of the *Thaumarchaeota* often contain *crenarchaeol*, a unique monolayer membrane lipid having four cyclopentyl rings and one cyclohexyl ring (Figure 2.3*b*). Despite the molecular

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differences between archaeal membranes and bacterial/eukaryotic membranes, their basic structural properties are the same in that each possesses hydrophobic interior hydrocarbon chains attached to polar (hydrophilic) glycerophosphate molecules.

Although molecular adaptations of membranes to high and low temperatures are discussed in some detail in Chapter 4, this may be a good opportunity to introduce the topic of saturated versus unsaturated hydrocarbon chains and discuss how they relate to membrane fluidity under high and low temperature extremes (e.g., why vegetable shortening is a solid at room temperature, and vegetable oil is a liquid under the same conditions).

The major functions of the cytoplasmic membrane are summarized in Figure 2.4 and include its role as (1) a *permeability barrier*, (2) a *protein anchor*, and (3) a means of *energy conservation*. With respect to acting as a permeability barrier, impress upon students that even extremely small ions do not freely pass through the hydrophobic interior of the membrane due to their charges. Therefore, most substances must be carried in and out by *transport proteins*. As stated in the text, transport proteins accumulate solutes against the concentration gradient (Figure 2.5). While water molecules do diffuse through membranes (due to their small size and only weak polarity) in a process called *osmosis*, the movement of water across membranes is greatly accelerated by water transport proteins called *aquaporins*. The porins will be more discussed in Section 2.4.

Introduce students to the concept that a membrane can function much like a battery in that it can store potential energy. By separating protons to the outside of the membrane from hydroxyl ions on the inside, the membrane becomes "energized" (Figure 2.4*c*), and this energized state is referred to as the *proton motive force (PMF).* The dissipation of this force results in the conversion of potential energy to kinetic energy. When protons stored outside of the membrane return to the inside of the cell through an ATP synthase enzyme complex, ADP and P_i are converted to ATP, the cell's chemical energy currency. This concept will be discussed in detail in Chapter 3.

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Discuss with your students the necessity for membrane-bound transport proteins by comparing the rate of simple diffusion of a solute across a membrane to the greatly accelerated rate of carrier-mediated transport of a solute across a membrane (Figure 2.5). Transport proteins allow for the accumulation inside a cell of a solute that may be in very low concentration in the environment. Point out that carrier-mediated transport proteins may show high or low specificity for a given solute, but in either case, the movement of molecules across the membrane is typically faster with a transporter than by simple diffusion alone.

Some students may find the variety of nutrient transport mechanisms difficult to comprehend initially, so discuss these mechanisms in detail using Figure 2.6 to illustrate the concepts and provide examples of each type of transport event (Section 2.2). When describing the three classes of membrane-bound *active transport* systems—*simple transport*, *group translocation*, and the *ABC (ATP-binding cassette) system*—highlight the following points to your students:

- Some transport mechanisms require only a membrane-spanning component (e.g., the simple transporters shown in Figure 2.6). Here, energy from the proton motive force (PMF) drives the transport event.
- Some require a series of proteins that cooperate in a phosphorylation/dephosphorylation cascade to carry out the transport event (e.g., the group translocation *phosphotransferase system*; Figure 2.6). An energy-rich

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phosphorylated compound, such as phosphoenolpyruvate, drives transport in this case.

- Some require a membrane-spanning transporter, a periplasmic substrate-binding protein, and an ATP-hydrolyzing protein to drive transport of the substrate (e.g., the monosaccharide ABC transporters; Figure 2.6).

The bacterial cell wall warrants extensive coverage in the classroom. Research on its structure and function can be traced back to the early history of microbiology. It began with the early observation of the differential reaction of various bacterial cells to the Gram stain. This stain distinguished two types of bacteria based on the composition of the cell wall: *gram-positive* and *gram-negative*. Research proceeded with the discovery that penicillin and other antibiotics target bacterial cell wall synthesis and induce cell lysis. Since humans do not have a cell wall and *peptidoglycan* is unique only to the bacterial cells, these classes of antibiotics are very beneficial for treating bacterial infections. These discoveries increased our understanding of prokaryotic cells and helped to obtain better chemotherapy with which to combat bacterial diseases. The mechanisms of peptidoglycan biosynthesis, cell division (covered in Chapter 4), osmotic lysis, and the activity of penicillin are important topics of discussion because they provide striking examples of the interrelationship of basic knowledge and practical applications of great significance. Impress upon your students that prokaryotic cells need a rigid cell wall in order to withstand the *turgor pressure,* otherwise they would burst and die.

Figure 2.7 provides an excellent summary of the differences in structure and appearance of *gram-positive* versus *gram-negative* cell walls (Section 2.3). Point out the fundamental repeating structure of peptidoglycan (the *glycan tetrapeptide*; Figure 2.8), which consists of alternating *N-acetylglucosamine* (NAG) and *N-acetylmuramic acid* (NAM) residues. Indicate that the latter of these two sugars is connected to a short peptide chain consisting of four amino acids, including in many bacteria the unique lysine analog diaminopimelic acid (DAP). The peptide chains provide structural rigidity to peptidoglycan by cross-linking the polysaccharide layers such that tensile strength is conferred on the cell wall in both the X and Y directions (Figure 2.9*a* and *c*). Although there is some variation in the amino acid composition of these peptide cross-linkages, there is great unity within the bacteria regarding the presence of *N*-acetylmuramic acid, DAP (which may be replaced by lysine), and D-amino acids (D-alanine and D-glutamic acid) rather than the usual L stereoisomers found in proteins. However, in contrast to gram-negative bacteria, some NAM residues in the peptidoglycan of gram-positive bacteria contain covalently bound *teichoic acids*, polyalcohols joined by phosphate esters (Figure 2.10). At this time, you may want to foreshadow the structure of the gram-positive bacterial cell wall in the context of antibiotic therapy and design. Emphasize that examples of unique cell chemistry often provide targets for successful chemotherapy without the problems of host toxicity. The mechanisms of action of both lysozyme and penicillin are good examples of how a chemical agent can destroy peptidoglycan, resulting in bacterial cell lysis.

Cell walls of *Archaea* do not contain peptidoglycan, but they do possess diverse chemistries that include proteins, polysaccharides, and glycoproteins. Some methanogens (Chapter 17) produce a polysaccharide similar to peptidoglycan called *pseudomurein* (Figure 2.11). Point out that the β-1,3 glycosidic linkage in pseudomurein is different from the β-1,4 linkage in peptidoglycan (compare Figures 2.9 and 2.11), thus making the former

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insensitive to the action of lysozyme. There are no known human pathogens from the *Archaea*, and thus the evolution of lysozyme most probably arose from the interactions of *Bacteria* with animal hosts over time.

The outer membrane of gram-negative bacteria is obvious in TEM sections, where it is seen as a wavy lipid bilayer outside of a thin layer of peptidoglycan. In the outer membrane, *lipopolysaccharide* (*LPS*) (Figure 2.12) replaces most of the phospholipids in the outer leaflet, whereas lipoproteins in the inner leaflet function to anchor the outer membrane to peptidoglycan (Figure 2.12). Depending upon the chemistry background of your students, discuss the chemical components of the LPS: (1) *Lipid A*, the phosphoglycolipid portion of the LPS; (2) the *core polysaccharide,* consisting of ketodeoxyoctonate (KDO), heptoses (7-carbon sugars), hexoses, and *N*-acetylglucosamine; and (3) the *O-polysaccharide*, consisting of repeating sequences of hexoses that form long chains and may be branched (Figure 2.13).

Although the purpose of the outer membrane is structural, it is toxic to animals due to the lipid A component of LPS. These toxic components are called *endotoxins*. Provide examples for your students of endotoxic human pathogens (e.g., *Shigella*, *Salmonella*, and *Escherichia*) that elicit ill effects in the host, including fever, gastrointestinal distress, and septic shock.

In contrast to the cytoplasmic membrane, the outer membrane is permeable to small molecules due to membrane channels called *porins* (Figure 2.12*a* and *c*), which vary in specificity from nonspecific to highly specific. Students should be made aware that the *periplasm* (Figure 2.12*a* and *b*) of gram-negative bacteria contains binding proteins that are not present in gram-positive bacteria. The periplasm contains a number of different classes of enzymes, some of which facilitate transport (Section 2.2) or chemotaxis (Section 2.11). Although not all *Archaea* contain pseudomurein, nearly all contain a cell wall of some type (exceptions were noted in Section 2.3). *Archaea* (and many *Bacteria*) have a paracrystalline surface layer, the *S-layer* (Section 2.5) composed of protein or glycoprotein (Figure 2.14). Discuss the potential functions of S-layers, which are varied and may include protecting the cell from osmotic lysis; preventing the access of larger particles, such as viruses, to the cytoplasmic membrane; and retaining secreted proteins near the cell surface. Also, impress on your students that a range of different configurations of the cell envelope exist. Use Figure 2.15 to explain this more in detail. Finally, note that there are also prokaryotic cells that lack a cell wall, including the mycoplasmas, a group of pathogenic bacteria (Figure 2.15*d*), and species of the archaeal genera *Thermoplasma* and *Ferroplasma* (see Chapter 17). As previously noted, the mycoplasmas are unusual among bacteria in that they contain sterols in their cytoplasmic membranes. The structural rigidity provided by these molecules presumably helps to maintain cell integrity during mild osmotic stress.

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2.6–2.8 | Cell Surface Structures and Inclusions

Cell surface structures produced by bacteria that are not an integral part of the cell wall are generally not considered essential to cell survival. However, the presence of *capsules* and *slime layers* (Figure 2.16), *fimbriae* (Figure 2.17), and *pili* (Figure 2.18) on many prokaryotes suggests that such structures play important ecological roles for these organisms, including the establishment of pathogenic associations with host cells (Section

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2.6). Additionally, outer surface layers have other functions, such as the protection from desiccation and the assisting biofilm formation. Although details of host–pathogen interaction are not part of the material presented here, you could pique student interest by showing a specific example of the role played by these cell surface structures in a specific pathogenesis (e.g., *Bacillus anthracis* and *Streptococcus pneumoniae*). Clearly define the structural and functional differences of fimbriae, pili, and flagella for students so that they do not equate these structures based on their similar microscopic appearance. Lastly, point out the unique attachment structures, called *hami*, of the SM1 group of *Archaea* (Figure 2.19*a, b*). These molecular grappling hooks, which resemble type IV pili in *Bacteria*, facilitate the formation of a dense biofilm network that may help trap nutrients in their deep subsurface habitat.

Many bacterial cells contain inclusions that mostly function as a storage of energy or nutrients (Section 2.7). For example, the storage granules *poly-β-hydroxyalkanoate* (*PHA*, of which *poly-β-hydroxybutyric acid* [*PHB*] is one type; Figure 2.20) and *glycogen*, both serve as carbon and energy reserves. Additional nutrient inclusions include *polyphosphate* and *elemental sulfur* granules (Figure 2.21*a, b*). The latter of these inclusions serves as an important secondary energy source for a variety of phototrophic and chemolithotrophic *Bacteria* that oxidize sulfide (H_2S) and other reduced sulfur compounds as electron donors (see Chapter 14). Other storage inclusions are not necessarily for nutritional purposes. Many prokaryotes catalyze *biomineralization*, the process of mineral formation by microorganisms. Figure 2.22 shows a beautiful example of benstonite granule accumulation inside a cell of the cyanobacterium *Gloeomargarita*; the function of these structures is unknown but it may be to provide ballast for the cell in its aqueous environment.

Gas vesicles are rigid, hollow structures in the cytoplasm of some cells that allow for vertical migration in a water column. They are therefore considered a mechanism of motility (Figure 2.23). The most known example of gas-vesiculate microbes are cyanobacteria, which form *blooms* near or on the lake surface (Figure 2.23*a*). Gas vesicles vary in size in different species. They can be as long as 1000 nm and as wide as 120 nm. The proteinaceous shell is permeable to gases but not to water and solutes.

A discussion of magnetosomes and *magnetotactic bacteria* should be of interest to students, who will likely find the idea of "magnetic bacteria" intriguing. Although the function of magnetosomes is also unknown, they are most certainly important to species that form them (Figure 2.24). Magnetotactic bacteria migrate along Earth's magnetic field lines by the process called *magnetotaxis*, which will be more discussed in Section 2.12.

Introduce Section 2.8 by emphasizing that many microbes produce spores, which allow them to survive harsh environmental conditions. *Endospores* are specialized, dormant cells that can tolerate desiccation, high temperatures, toxic chemicals, radiation, and nutrient depletion (Figure 2.25). To spark student interest, note that many endospore-forming bacteria are also pathogenic and cause some of the most serious diseases known. For example, pathogenic members of the genera *Bacillus* and *Clostridium* often produce potent toxins that cause fatal diseases if not treated within a short time. Examples include botulism (*C. botulinum*), tetanus (*C. tetani*), gas gangrene (*C. perfringens*), gastroenteritis (*C. difficile*), and anthrax (*B. anthracis*). Infection caused by endospore-forming bacteria will be discussed more in detail in Chapters 32 and 33.

Depending on the level of your course, discuss the structure of endospores and the *endosporulation* and *germination* processes in some detail (Figures 2.26–2.29). Compare and contrast endospores versus vegetative cells. Key points to stress include the following:

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- Mention that the *germination* process occurs in three steps: activation, germination, and outgrowth (Figure 2.27).
- As illustrated in Figure 2.28, describe four layers of endospore. Emphasize the unique nature of the core, stressing the functions of the *dipicolinic acid* and calcium (Ca^{2+}) complexes, the low water content, and the role of *small acid-soluble spore proteins* (SASPs) in protecting the DNA and in serving as a carbon and energy source for the cell during germination.
- Discuss endospore formation as an example of cellular differentiation in prokaryotes, using *Bacillus subtilis* as a model (Figure 2.29). To impress upon students the remarkable complexity of the differentiation process, mention that more than 200 genes are involved in sporulation, and many details of the process are still being investigated in laboratories around the world.
- Point out the key differences between vegetative cells, which are metabolically active and dividing cells, and endospores, which are essentially dormant cell forms that exhibit minimal enzymatic activity (Table 2.1).

Finally, students should show interest in a discussion concerning how long endospores can remain viable. The debate on the longevity of these structures has now pushed their life span to millions of years. If experimental evidence from independent research laboratories repeatedly supports these claims, this would indeed be an extraordinary testament to the life-preserving design of these structures.

2.9–2.12 | Cell Locomotion

The ability of *Bacteria* to move via *flagella* (or *Archaea* to move via *archaella*) is intimately connected to their ability to sense and respond to environmental signals through complex signal transduction pathways (Section 2.9). Flagella are arranged in a variety of ways on the cell surface (Figures 2.30 and 2.31). Some bacteria can have a group of many flagella called *tufts* (Figure 2.32). Rather than moving in a whip-like motion like the flagella of eukaryotes, bacterial flagella and archaella *rotate* to propel the cell (Figure 2.33). Mention to your students that the cheetah can move at about 25 body-lengths/sec, while the flagella can support a swimming body speed of up to 60 cell-lengths/sec! Point out the fact that for many species, the rotation is reversible, and the direction of the rotation dictates whether the cell moves forward (called a *run*), backward, or tumbles in place; the latter occurs for cells having peritrichous flagellation (multiple flagella arranged all around the cell).

The flagellar structure is complex, and its synthesis and assembly involve more than 50 genes in *Escherichia* and *Salmonella* species. Rotation of bacterial flagella requires significant energy directly from a *proton motive force* (*PMF*; Section 2.1). In fact, a single rotation requires the translocation of about 1200 protons across the cytoplasmic membrane through the *basal body* (Figure 2.34). Using Figure 2.35, discuss the biosynthesis of the flagella step by step.

Flagella from the different domains of life exhibit significant structural and operational differences. For example, bacterial flagella are about twice as thick as archaella. Archaella measure about 10–13 nm in width (Figure 2.36). In addition, the filament portion of all bacterial flagella is composed of a single type of flagellin protein, whereas the number of proteins that compose archaellar filaments varies depending on the species. Because of their structural similarity, the *archaellum* has been likened to a rotating version of the type IV

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pilus of bacteria, an ATP-powered appendage that allows for twitching motility (Sections 2.6 and 2.10). As such, archaellar rotation is powered directly by the hydrolysis of ATP rather than by a PMF, as is the case for bacterial flagella. The fundamental differences among bacterial flagella, eukaryotic flagella, and archaella suggest that these mechanisms of motility have arisen independently as a result of convergent evolution rather than from a common origin.

Section 2.10 introduces the concept of surface motility. Start by explaining that surface motility is not the same as swimming motility and it requires attachment to a surface (Figure 2.37). Some bacteria exhibit the *twitching motility*, in which cell movements are carried out by the repeated extension and retraction of type IV pili (see Section 2.6) in a grappling hook style of motion (Figure 2.38*a*). The type IV pili requires ATP hydrolysis in order to extend and then retract, which causes a movement forward. Twitching ability has been described in *Pseudomonas* and myxobacteria. Mention the interesting fact about myxobacteria, a predatory bacteria that perform two types of motility: social and adventurous motility.

Gliding motility (motility without flagella; Figure 2.38*b*) in bacteria is a relatively underrepresented phenomenon in microbiology texts, and this is probably because of the lack of knowledge of the molecular mechanisms involved in the process. Consequently, it is a good puzzle to present to students following your discussion of flagellar locomotion, about which much is known. Gliding motility has never been observed in *Archaea*, but several species of gliding *Bacteria* are known, with key examples including species of cyanobacteria and the genera *Myxococcus* and *Flavobacterium* (Figure 2.37*c*). Movement by gliding requires a solid surface and is considerably slower than flagellar motility. Several mechanisms of gliding motility have been described. Gliding motility requires helical intracellular protein track that interacts with gliding motors and extracellular adhesion proteins (Figure 2.38*b*). Although, the exact mechanism of gliding is still unknown.

The ability of bacteria to exhibit *taxis* (i.e., directed movement) confers a selective advantage depending upon environmental conditions. Students should understand that, unlike larger organisms, microorganisms sense gradients in a *temporal* (an effect lasting for only a short time) rather than a *spatial* (a lingering effect) manner. In other words, they must continually compare their current external conditions with those of a few moments before. The studies of chemotaxis in *E. coli* provided the first genetic model of the process in swimming bacteria (Section 2.11). Chemotaxis will be discussed in Section 7.6 in the context of two-component signal transduction systems, but use Figure 2.39 to show the run and tumble "directed" response and capillary assay system used to evaluate and identify signal molecules that act as attractants or repellants. Discuss the ways of observing and measuring chemotaxis. Focus on capillary tube assay and explain how it works (Figure 2.40).

In Section 2.12, discuss other forms of taxis. Many of the protein components that function in chemotactic pathways are also activated during *phototaxis*, and flagellar rotation is controlled accordingly. The response of *Rhodocista centenaria* (Figure 2.31) to light is a fascinating example of phototaxis. Mention to students that *scotophobotaxis* (movement away from dark) is not the same as true phototaxis, which involves movement up a light gradient (Figure 2.41*b*). *R. centenaria* is also unusual in that an entire colony of cells on solid media will move toward an infrared light source (the wavelengths absorbed by their photosynthetic pigments) and away from fluorescent light. If one observes the cells

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within the colony as the colony moves in one direction, the individual cells appear to be moving more or less randomly, suggesting that there must be some intercellular communication occurring to generate a net directional movement.

Other types of taxis have been observed in microorganisms, including directed movement toward or away from oxygen (*aerotaxis*), toward a specific osmotic condition (*osmotaxis*), or toward water (*hydrotaxis*). Point out that some aerobic bacteria that exhibit aerotaxis contain magnetosomes, which act like a compass, pulling the organism downward toward the Earth's magnetic poles and into the sediments where dissolved oxygen (O_2) concentrations are lower.

2.13–2.15 | Eukaryotic Microbial Cells

Students should be familiar with the organelles and general structure of the eukaryotic cell from general biology courses, but you should still present a brief overview of the topic, focusing first on the nucleus and chromosome organization (Figures 2.42 and 2.43). Remind students that eukaryotic DNA is packaged in the nucleus by being wound around positively charged *histone* proteins. Note that transport of proteins and nucleic acids through *nuclear pores* requires the energy of GTP. The *nucleolus* is the site of ribosomal RNA (rRNA) synthesis and assembly of the large and small subunits of the ribosome. Also review *mitosis* (Figure 2.44) and *meiosis* with your students, reminding them that these processes, which occur only in eukaryotes, are mechanisms by which a cell divides to create two diploid daughter cells or four haploid gametes (or spores), respectively.

In Section 2.14, review mitochondrial structure and function with your students. Point out that *mitochondria* are the size of a typical bacterium and they contain their own DNA and ribosomes (Figure 2.45). Therefore, mitochondria reproduce independently of the cell. Mention *cristae*, internal membranes containing enzymes needed for respiration.

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Chloroplasts are the structures found in plant cells and many microbial eukaryotes (e.g., dinoflagellates, euglenoids, diatoms, and various algae) that carry out photosynthesis and allow for photoautotrophic growth. Like mitochondria, chloroplasts contain their own DNA and ribosomes, and are visible with the light microscope (Figure 2.46). The relationship of chloroplasts and mitochondria to *Bacteria* is well documented and is discussed briefly here as the *endosymbiotic theory*. Although this topic will be addressed in more detail in future chapters (see Sections 13.4 and 18.1), you may wish to point out key features supporting endosymbiosis to your students at this time:

- Both structures (mitochondria and chloroplasts) contain their own DNA in covalently closed circles. This DNA encodes rRNAs, transfer RNAs (tRNAs), and some respiratory enzymes.
- These organelles contain their own ribosomes that are bacterial in structure and are sensitive to antibiotics that affect bacterial ribosomes.
- The nuclear DNA of eukaryotic cells contains bacterially derived genes, lending additional evidence to support the endosymbiotic hypothesis (Section 18.1).
- 16S rRNA gene sequence analyses show the evolutionary relatedness of these structures to *Bacteria*.

Finally, review the function of other eukaryotic cell structures (e.g., the endoplasmic reticulum, Golgi complex, lysosomes, cytoskeletal elements, flagella, and cilia) mentioned in Section 2.15, which should already be familiar to most students. Emphasize that protein filaments, including microtubules, microfilaments (Figure 2.47), and intermediate

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filaments form the cell cytoskeleton. Point out that eukaryotic flagella are powered by ATP hydrolysis and propel the cell via a whip-like motion (Figure 2.48*a*) rather than by rotation, as seen in bacterial flagella and archaella (Section 2.9).

Answers to Review Questions

1. The cytoplasmic membrane is composed of a phospholipid bilayer, which consists of a hydrophilic head group and hydrophobic tails. *Bacteria* have ester linkages that bind the fatty acid tails to glycerophosphate head, while lipids of *Archaea* have isoprenoid tails (rather than fatty acid tails), which are bound to glycerol by ether linkages. Additionally, some *Archaea* can have a lipid monolayer instead of a bilayer. The cytoplasmic membrane has several transport proteins that carry substances in and out of the cell.
2. Lactose in *E. coli* is transported by simple transport, where a lac permease is a symporter that helps to transport lactose. This process is driven by the energy in the proton motive force. Glucose is transported by using group translocation transporters. The phosphotransferase translocation system has five proteins including Enzyme I, Enzymes II_a, II_b, II_c, and HPr. The chemical modification of glucose is driven by phosphoenolpyruvate. Maltose is transported via ABC transporter, which consists of three components: a binding protein, a transmembrane protein, and cytoplasmic ATP-hydrolyzing protein. The substrate transport is driven by ATP.
3. Because the rigid layer is a polymer composed of sugars linked by β-1,4 glycosidic bonds and polypeptides that cross-link *N*-acetylmuramic acid and *N*-acetylglucosamine residues, the term peptidoglycan ("protein" + "sugar") is appropriate. Together, the covalent glycosidic and peptide bonds of peptidoglycan provide tensile strength in both the X and Y directions, respectively, to protect against osmotic lysis and maintain cell shape.
4. Functions of the outer membrane of gram-negative bacteria include antigenicity, adhesion to surfaces, toxicity for animals, provision of membrane channels and porins for the influx and efflux of low molecular weight substances, and a permeability barrier to the passage of high molecular weight substances. The chemical composition of the outer membrane is a phospholipid bilayer containing LPS. The endotoxin lipid A is the lipid portion of the LPS. It consists of fatty acids connected through amine groups to a disaccharide composed of glucosamine phosphate.
5. S-layers consist of protein or glycoprotein in a paracrystalline array. They are found in both *Bacteria* and *Archaea* and may serve as an outermost selective sieve around the cell to prevent access of large particles, such as viruses, to the cytoplasmic membrane.
6. Polysaccharide layers produced by bacteria are referred to as capsules and/or slime layers, and they have several potential functions. They play a major role in the attachment of cells to a surface (a property that allows for biofilm formation); they prevent phagocytosis by immune system macrophages; and they function to prevent desiccation.
7. Poly-β-hydroxybutyrate granules serve as a cell energy and carbon reserve and consist of a polymeric fatty acid, whereas magnetosomes consist of magnetite or greigate and serve as small magnetic compasses. Aquatic cells may use magnetosomes as a means to align themselves within zones of favorable oxygen concentration.
8. An endospore differs from a vegetative cell for several reasons. The cytoplasm of endospores is considerably dehydrated compared to vegetative cells, and endospores have a

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unique cell surface consisting of multiple layers of proteins. In addition, endospores are "shut down" in the sense that they are essentially metabolically dormant. All of these factors permit significant resistance to heat, radiation, desiccation, toxic chemicals, and extremes of pH, and they allow for remarkable longevity of these structures. A distinctive characteristic of endospore is dipicolinic acid that is absent in other spores. Likewise, endospores are the only type of spore that can tolerate high heat.

9. The bacterial flagellum is a long, rigid, protein filament of polymerized flagellin that extends from the cytoplasmic membrane and cell wall. It generates cellular motility by rapidly rotating, much like a miniature propeller. A wider hook at the base of the flagellum serves to connect the flagellum to the motor portion (basal body), which is anchored to the cell wall and cytoplasmic membrane. In *Bacteria*, the proton motive force provides the energy for rotation via the flow of protons across the membrane. Archaella are thinner by comparison and may be composed of several proteins that show homology to the type IV pilus of *Bacteria*. In addition, unlike bacterial flagella, archaellar rotation is driven by ATP hydrolysis.

10. The gliding motility exhibited by species of *Flavobacterium* differs from the swimming motility of *E. coli* and twitching motility of *Pseudomonas* in several respects. Gliding motility, which requires a surface for the cells to move across, is considerably slower than the swimming motility of flagellated cells. The mechanism of gliding in *Flavobacterium* appears to be by a ratcheting movement between proteins anchored in the cytoplasmic membrane and the outer membrane. However, gliding motility in species of *Flavobacterium* and swimming motility in *E. coli* are both powered by energy from the proton motive force. Twitching motility exhibited by *Pseudomonas* requires type IV pili, which attaches to a surface and then pulls and retracts moving the microorganism forward. This movement is mediated by ATP hydrolysis.

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11. Motile bacteria move toward attractants by comparing the strength of stimuli (using chemoreceptors). If an environmental stimulus is desirable, flagellar activity results in fewer tumbles and longer runs. If a stimulus is not desirable, then the opposite will occur. Although the new direction following a tumble is random, adjusting the duration of runs and the frequency of tumbles allows the cell to ultimately move toward the attractant, albeit in a somewhat erratic manner. Chemotaxis, therefore, resembles smell rather than sight.

12. Magnetotactic bacteria are aerobic microorganisms that require a low O_2 concentration (1–5%) for survival. Magnetosomes help the bacteria to position themselves with magnetic field lines. This magnetic alignment allows for migration toward an optimal O_2 concentration.

13. Three features that clearly differentiate eukaryotic from prokaryotic cells are the following: (1) Almost all eukaryotes possess a membrane-bound nucleus containing their genomic DNA; (2) unlike nearly all prokaryotes, eukaryotic cells contain various membrane-bound organelles (e.g., mitochondria and the Golgi complex); and (3) eukaryotic cells lack a cell wall and instead of that they have a cytoplasm membrane, which contains sterols.

14. The fact that mitochondria and chloroplasts contain their own circular DNA genomes and ribosomes that are more similar to bacterial ribosomes than eukaryotic, supports the endosymbiotic hypothesis. Also, mitochondria and chloroplasts are about the same size as *Bacteria* and are visible with the light microscope. In addition, both mitochondria and

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chloroplast have the same function, they provide ATP to the eukaryotic cell.

15. Both eukaryotic and bacterial flagella function as motility structures. However, they differ structurally. Eukaryotic flagella are much larger than bacterial and move in a whip-like motion due to the activity of cytoskeleton proteins, while bacterial flagella are smaller, rigid and helical, and move by rotation.

Answers to Application Questions

1. Listed below are a few ways to distinguish *Bacteria* and *Archaea*:

Bacteria

Ester linkages between fatty acid tails and glycerol

Fatty acids tails in cytoplasmic membrane

N-acetylglucosamine and *N*-acetylmuramic acid

Peptidoglycan in cell wall

Lysozyme and antibiotic sensitive

Archaea

Ether linkages between isoprenoid tails and glycerol

Isoprenoid tails in cytoplasmic membrane

N-acetylglucosamine and *N*-acetyltalosaminuronic acid

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Pseudomurein in cell wall

Lysozyme and antibiotic resistant

2. Many antibiotics target peptidoglycan in the bacterial cell wall and therefore are effective against gram-positive bacteria. However, gram-negative bacteria have only one thin layer of peptidoglycan and additionally they contain an outer membrane. The outer membrane is surrounded by a slime layer, which prevents antibiotics from entering into the cell. Porins are protein channels that are present in the outer membrane. Therefore, in order to effectively treat the infection caused by a gram-negative bacteria, one must chemically modify porins, which would affect outer membrane permeability and allow antibiotics to enter the cell.

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