

I • Cells of *Bacteria* and *Archaea*

In the opening chapter, we painted a picture of the microbial world using a broad brush. There we considered in a very general way several key aspects of microbiology essential to a modern understanding of the science. In Chapter 2, we move on to begin a more detailed examination of microbial life, with a focus on cell structure and function.

Microscopic examination of microorganisms immediately reveals their shape and size. A variety of cell shapes pervade the microbial world, and although microscopic by their very nature, microbial cells—both prokaryotic and eukaryotic—come in a variety of sizes. Cell shape can be useful for distinguishing different microbial cells and often has ecological significance. Moreover, the very small size of most microbial cells has a profound effect on their ecology and dictates many aspects of their biology. We begin by considering cell shape and then consider cell size.

2.1 Cell Morphology

In microbiology, the term **morphology** means cell shape. Several morphologies are found among *Bacteria* and *Archaea*, and the most common ones are described by terms that are part of the essential lexicon of the microbiologist.

Major Morphologies of Prokaryotic Cells

Common morphologies of prokaryotic cells are shown in **Figure 2.1**. A cell that is spherical or ovoid in morphology is called a *coccus* (plural, cocci). A cylindrically shaped cell is called a *rod* or a *bacillus*. Some cells form curved or loose spiral shapes and are called *spirilla*. The cells of some *Bacteria* and *Archaea* remain together in groups or clusters after cell division, and the arrangements are often characteristic. For instance, some cocci form long chains (for example, the bacterium *Streptococcus*), others occur in

three-dimensional cubes (*Sarcina*), and still others in grapelike clusters (*Staphylococcus*).

Some morphological groups are immediately recognizable by the unusual shapes of their individual cells. Examples include the spirochetes, which are tightly coiled *Bacteria*; bacteria that form extensions of their cells as long tubes or stalks (appendaged forms); and filamentous bacteria, which form long, thin cells or chains of cells (Figure 2.1).

The cell morphologies described here are representative but certainly not exhaustive; many variations of these morphologies are known. For example, there can be fat rods, thin rods, short rods, and long rods, a rod simply being a cell—roughly in the shape of a cylinder—that is longer in one dimension than in the other. As we will see, there are even square bacteria and star-shaped bacteria! Cell morphologies thus form a continuum, with some shapes, such as rods and cocci, being very common, whereas others, such as spiral, budding, and filamentous shapes, are less common.

Morphology and Biology

Although cell morphology is easily determined, it is a poor predictor of other properties of a cell. For example, under the microscope many rod-shaped *Archaea* are indistinguishable from rod-shaped *Bacteria*, yet we know they are of different phylogenetic domains (see Section 1.13). With rare exceptions, it is impossible to predict the physiology, ecology, phylogeny, pathogenic (disease-causing) potential, or virtually any other major property of a prokaryotic cell by simply knowing its morphology. Nevertheless, cell morphology is an important characteristic that is always noted when describing a particular species of *Bacteria* or *Archaea*.

Why are the cells of a given species the shape they are? Although we know quite a bit about *how* cell shape is controlled, we know relatively little about *why* a particular cell displays the morphology it does. The morphology of a given microbe is undoubtedly the result of the selective forces that have shaped its evolution to

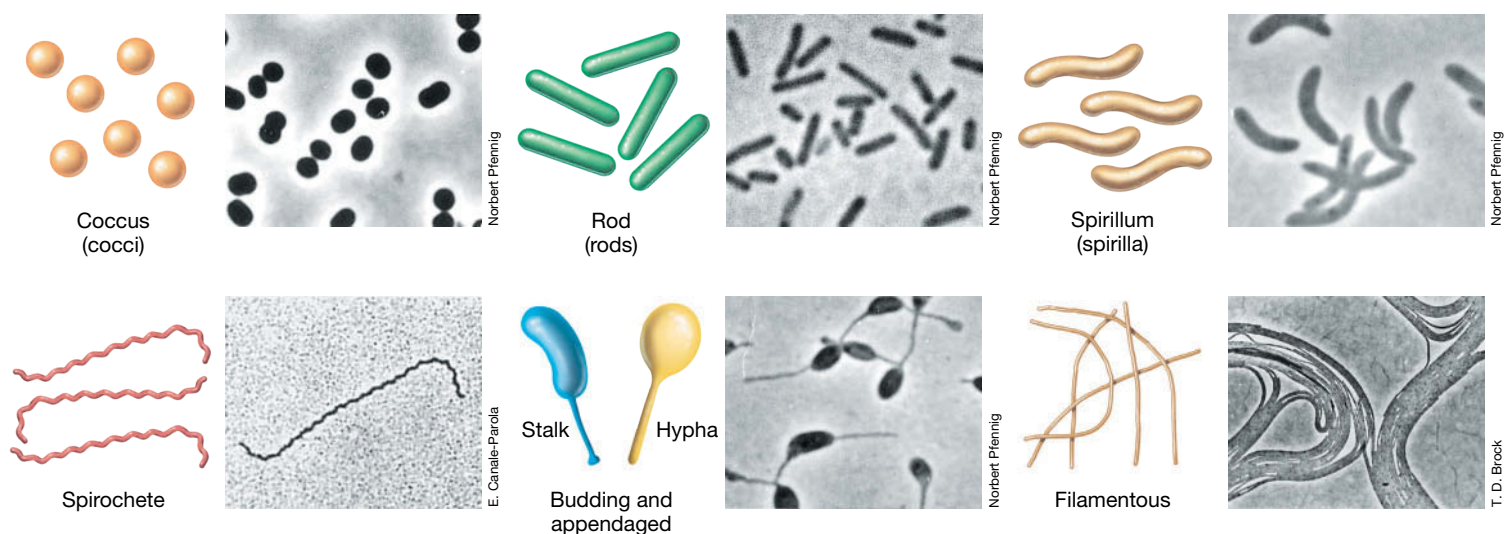


Figure 2.1 Cell morphologies. Beside each drawing is a phase-contrast photomicrograph of cells showing that morphology. Coccus (cell diameter in photomicrograph, 1.5 μm); rod (1 μm); spirillum (1 μm); spirochete (0.25 μm); budding (1.2 μm); filamentous (0.8 μm). All photomicrographs are of species of *Bacteria*. Not all of these morphologies are known among the *Archaea*, but cocci, rods, and spirilla are common.

maximize fitness for competitive success in its habitat. Some examples of these might include evolving an optimal cell shape to maximize nutrient uptake for survival in nutrient-limiting environments (small cells and others with high surface-to-volume ratios, such as appendaged cells), evolving a morphology to exploit swimming motility in viscous environments (helical- or spiral-shaped cells), or evolving a morphology that facilitates gliding motility along a surface (filamentous bacteria) (Figure 2.1).

MINIQUIZ

- How do cocci and rods differ in morphology?
- Using a microscope, could you differentiate a coccus from a spirillum? A pathogen from a nonpathogen?

2.2 The Small World

Cells of *Bacteria* and *Archaea* vary in size from as small as about 0.2 micrometer (μm) in diameter to those more than 700 μm in diameter (Table 2.1). The vast majority of rod-shaped species that have been cultured are between 0.5 and 4 μm wide and less than 15 μm long. A few very large *Bacteria* are known, such as *Epulopiscium fishelsoni*, whose cells exceed 600 μm (0.6 millimeter) in length (Figure 2.2a;  Figure 1.38). This bacterium, phylogenetically related to the endospore-forming bacterium *Clostridium* and found in the gut of the surgeonfish, contains multiple copies of its genome. The many copies are apparently necessary because the volume of an *Epulopiscium* cell is so large (Table 2.1) that a single copy of its genome would be insufficient to support its transcriptional and translational demands.

Cells of the largest known bacterium, the sulfur-oxidizing chemolithotroph *Thiomargarita* (Figure 2.2b), are even larger than those of *Epulopiscium*, about 750 μm in diameter; such cells are just visible to

the naked eye. Why these cells are so large is not well understood, although for sulfur bacteria a large cell size may have evolved for storing inclusions of sulfur (used as an energy source). No species of *Archaea* are known that rival *Epulopiscium* or *Thiomargarita* in cell size, but that may simply be because they remain undiscovered.

It is hypothesized that the upper size limit for prokaryotic cells results from the decreasing ability of larger and larger cells to transport nutrients (their surface-to-volume ratio is very small; see the next subsection). Since the metabolic rate of a cell varies inversely with the square of its size, for very large cells, nutrient uptake would eventually limit metabolism to the point that the cell would no longer be competitive with smaller cells.

Very large cells are uncommon in the prokaryotic world. In contrast to *Thiomargarita* or *Epulopiscium* (Figure 2.2), the dimensions of an average rod-shaped bacterium, such as *Escherichia coli*, for example, are about 1–2 μm ; these dimensions are typical of cells in the prokaryotic world. By contrast, eukaryotic cells can be as small as 2 to more than 600 μm in diameter, although very small microbial eukaryotes (cells less than about 6 μm in diameter) are uncommon. We explore the world of microbial eukaryotes in Chapter 18.

Surface-to-Volume Ratios, Growth Rates, and Evolution

For a cell, there are advantages to being small. Small cells have more surface area relative to cell volume than do large cells and thus have a higher *surface-to-volume ratio*. To understand this, consider a coccus-shaped cell. The volume of a coccus is a function of the cube of its radius ($V = \frac{4}{3}\pi r^3$), whereas its surface area is a function of the square of the radius ($S = 4\pi r^2$). Therefore, the *S/V* ratio of a coccus is $3/r$ (Figure 2.3). As cell size *increases*, its *S/V* ratio *decreases*. To illustrate this, consider the *S/V* ratio for some of the cells of different sizes listed in Table 2.1: *Pelagibacter ubique*, 22; *E. coli*, 4.5; and *E. fishelsoni* (Figure 2.2a), 0.05. These are all rods

TABLE 2.1 Cell size and volume of some cells of *Bacteria*, from the largest to the smallest

Organism	Characteristics	Morphology	Size ^a (μm) ³	Cell volume (μm) ³	Volumes compared to <i>E. coli</i>
<i>Thiomargarita namibiensis</i>	Sulfur chemolithotroph	Cocci in chains	750	200,000,000	100,000,000×
<i>Epulopiscium fishelsoni</i> ^a	Chemoorganotroph	Rods with tapered ends	80 × 600	3,000,000	1,500,000×
<i>Beggiatoa</i> species ^a	Sulfur chemolithotroph	Filaments	50 × 160	1,000,000	500,000×
<i>Achromatium oxaliferum</i>	Sulfur chemolithotroph	Cocci	35 × 95	80,000	40,000×
<i>Lyngbya majuscula</i>	Cyanobacterium	Filaments	8 × 80	40,000	20,000×
<i>Thiovulum majus</i>	Sulfur chemolithotroph	Cocci	18	3,000	1,500×
<i>Staphylothermus marinus</i> ^a	Hyperthermophile	Cocci in irregular clusters	15	1,800	900×
<i>Magnetobacterium bavaricum</i>	Magnetotactic bacterium	Rods	2 × 10	30	15×
<i>Escherichia coli</i>	Chemoorganotroph	Rods	1 × 2	2	1×
<i>Pelagibacter ubique</i> ^a	Marine chemoorganotroph	Rods	0.2 × 0.5	0.014	0.007×
Ultra-small bacteria	Uncultured, from groundwater	Variable	<0.2	0.009	0.0045×
<i>Mycoplasma pneumoniae</i>	Pathogenic bacterium	Pleomorphic ^b	0.2	0.005	0.0025×

^aWhere only one number is given, this is the diameter of spherical cells. The values given are for the largest cell size observed in each species. For example, for *T. namibiensis*, an average cell is only about 200 μm in diameter. But on occasion, giant cells of 750 μm are observed. Likewise, an average cell of *S. marinus* is about 1 μm in diameter. The species of *Beggiatoa* here is unclear and *E. fishelsoni*, *M. bavaricum*, and *P. ubique* are not formally recognized names in taxonomy.

^b*Mycoplasma* is a bacterium that lacks a cell wall and can thus take on many shapes (pleomorphic means “many shapes”).

Source: Data obtained from Schulz, H.N., and B.B. Jørgensen. 2001. *Annu. Rev. Microbiol.* 55: 105–137, and Luef, B., et al. 2015. *Nature Communications*. doi:10.1038/ncomms7372.

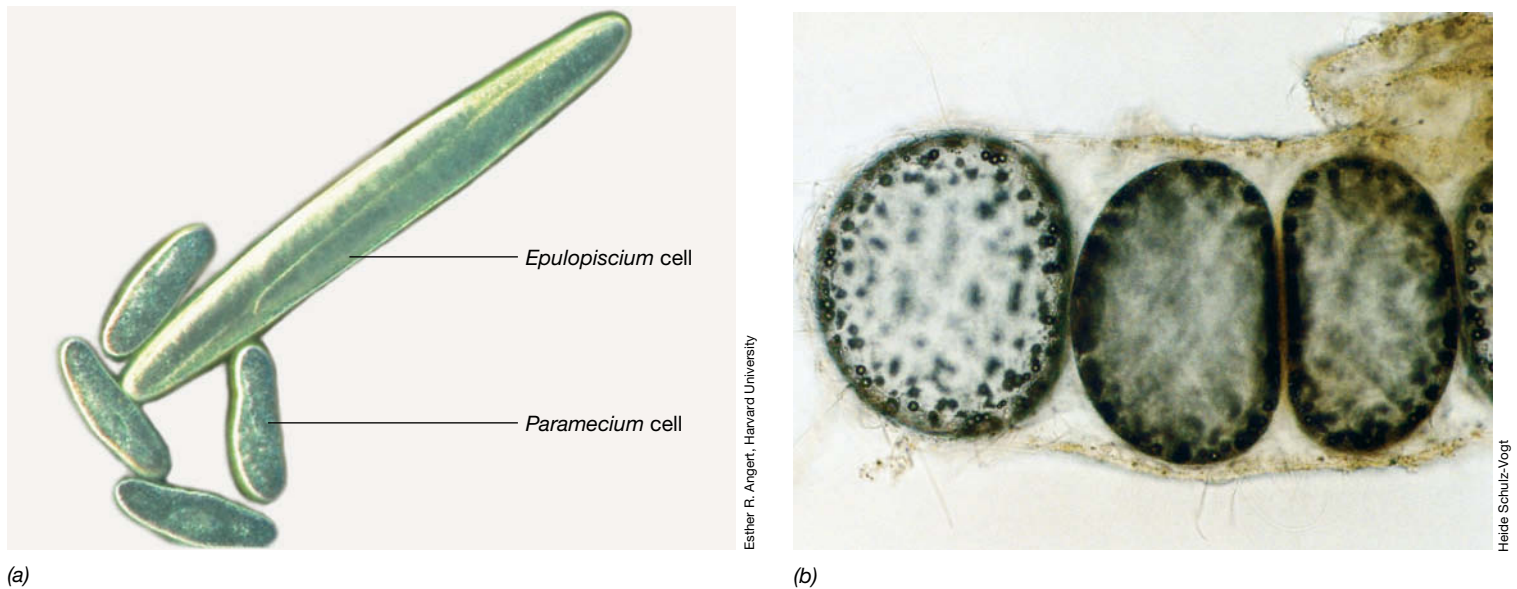


Figure 2.2 Two very large *Bacteria*. (a) *Epulopiscium fishelsoni*. The rod-shaped cell is about 600 μm (0.6 mm) long and 75 μm wide and is shown with four cells of the protist *Paramaecium* (a microbial eukaryote), each of which is about 150 μm long. (b) *Thiomargarita namibiensis*, a large sulfur chemolithotroph and currently the largest known of all prokaryotic cells. Cell widths vary from 400 to 750 μm .

rather than cocci, but if it is assumed that a rod-shaped cell is a perfect cylinder, the same S/V principles that hold for cocci also hold for rods; that is, for rods of a given length, cells with a smaller radius have a greater S/V than do cells with a larger radius.

The S/V ratio of a cell controls many of its properties, including its growth rate and evolution. Because how fast a cell can grow depends in part on the rate at which it can exchange nutrients and waste products with its environment, the higher S/V ratio of small cells supports a faster rate of nutrient and waste exchange per unit of cell volume compared with large cells. As a result, free-living smaller cells tend to grow faster than free-living larger cells, and for a given amount of resources (nutrients available to support

growth), a larger population of small cells than of large cells can be supported. This in turn can affect a cell's evolution.

Each time a cell divides, its chromosome replicates. As DNA is replicated, occasional errors, called *mutations*, occur. Because mutation rates are roughly the same in all cells, large or small, the more chromosome replications that occur, the greater the total number of mutations in the cell population. Mutations are the “raw material” of evolution; the larger the pool of mutations, the greater the evolutionary possibilities. Thus, because prokaryotic cells are quite small and are also genetically haploid (they typically have only one copy of each gene, allowing mutations to be expressed immediately), prokaryotic cells can grow faster and evolve more rapidly than can larger cells.

Because of their typically larger size, not only is the S/V ratio of microbial eukaryotes smaller, the diploid character of the eukaryotic cell (a cell has two copies of each gene) allows for a mutation in one gene to be masked by a second, unmutated gene copy. These fundamental differences in size and genetics between prokaryotic and eukaryotic cells help explain why species of *Bacteria* and *Archaea* adapt rapidly to changing environmental conditions and more easily exploit new habitats than do eukaryotic cells. We illustrate this concept in later chapters when we consider the enormous diversity of cells and metabolisms of *Bacteria* and *Archaea* (Chapters 14–17), the rapidity of prokaryotic evolution (Chapter 13), and the ecological ramifications of microbial activities in nature (Chapters 19–23).

Lower Limits to Cell Size

From the foregoing, one would predict that smaller and smaller microbes would have greater and greater selective advantages in nature and that as a consequence, only extremely tiny bacterial cells would exist. However, this is not the case, as there are lower limits to cell size and good reasons why there should be.

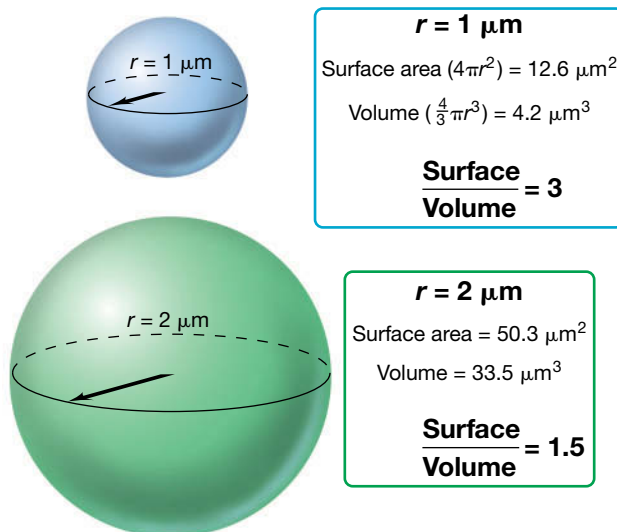


Figure 2.3 Surface area and volume relationships in cells. As a cell increases in size, its S/V ratio decreases.