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A magnificent braided river delta with communities of red and green flora showing at low tide. Alaska, Lower Cook Inlet, Kachemak Bay. From the NOAA photo library. Credit: Alaska ShoreZone Program, NOAA/NMFS/AKFSC, courtesy of Mandy Lindeberg.

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CHAPTER ONE

A Microbial Planet

KEY CONCEPTS

This chapter covers the following topics in the ASM Fundamental Statements.

EVOLUTION

- Cells, organelles (e.g., mitochondria and chloroplasts), and all major metabolic pathways evolved from early anucleated cells.
- Mutations and horizontal gene transfer, with the immense variety of microenvironments, have selected for a huge diversity of microorganisms.

CELL STRUCTURE AND FUNCTION

- The structure and function of microorganisms have been revealed by the use of microscopy (including bright-field, phase-contrast, fluorescent, and electron).
- While microscopic eukaryotes (for example, fungi, protozoa, and algae) carry out some of the same processes as bacteria, many of the cellular properties are fundamentally different.

METABOLIC PATHWAYS

- The survival and growth of any microorganism in a given environment depend on its metabolic characteristics.

MICROBIAL SYSTEMS

- Microorganisms are ubiquitous and live in diverse and dynamic ecosystems.
- Microorganisms, cellular and viral, can interact with both human and nonhuman hosts in beneficial, neutral, or detrimental ways.

IMPACT OF MICROORGANISMS

- Microbes are essential for life as we know it and the processes that support life (e.g., in biogeochemical cycles and plant and/or animal microflora).

Introduction

An invisible, yet ubiquitous influence, microbes connect the health of humans, animals, and ecosystems. The term "microbe" refers to those small organisms that are not visible to the unaided eye. Due to their relatively small size and simple design, microbes reproduce rapidly and adapt quickly to changes in their environment, making them the most abundant life form on Earth. Moreover, they were also the first organisms to colonize the planet almost 4 billion years ago, a time when Earth was inhospitable to most of life. Microbes interact with living and nonliving components of their environment, which drives their evolution in myriad ways. By diversifying and acquiring new properties, microbes not only adapt to the profound changes that the planet undergoes over the course of its long history but also influence environmental changes. Microbes now inhabit every corner of Earth; their impact is truly staggering (Table 1.1).

You may be familiar with microbes that cause disease, but these are only a small fraction of all the microbial diversity existing today. Microbes are in fact our greatest allies: they sustain the life of all other organisms and help us advance technology and cope with the profound effects that our own activities have on the planet. They are integral members of our lives and how we function (Table 1.2). To introduce the magnitude of their contributions to transforming Earth into the living planet of today and shaping our future world, in this chapter we describe microbes' most notable characteristics. We'll examine a world that is stunningly diverse, immense in size, and vast in its importance to all of us. You will not see our planet in the same way again.

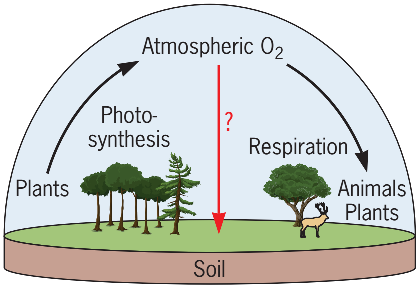
TABLE 1.1 Characteristics of microbes

- The source of all life forms
- More phylogenetically diverse than plants and animals
- Enormously abundant
- Inhabit virtually every place on Earth where there is liquid water
- Carry out transformations of matter essential for life
- Transform the geosphere
- Affect the climate
- Participate in countless symbiotic relationships with animals, plants, and other microbes
- Influence the behavior of animals and plants
- Cause disease

TABLE 1.2 Human use of microbes

- Carrying out chemical activities of major industrial importance
- Engineering for production of useful proteins, e.g., vaccines
- Enhancing food production and preservation
- Providing vital public health measures, such as sewage disposal
- Bioremediation of polluted sites
- Malevolent intent (biological warfare, bioterrorism)
- Source of heat-resistant enzymes

CASE: Where did the oxygen disappear to in the Biosphere 2 experiment?



Microbes have a global impact on life on Earth. It is easy to appreciate their significance by considering what went wrong in the Biosphere 2 project. In the early 1990s, scientists sought to build a closed ecosystem in Arizona within an airtight, glass-and-steel enclosure where plants and animals could sustain life. Daytime photosynthesis by the selected plants produced plenty of oxygen to support the nighttime consumption by both plants and animals in the enclosure. Nevertheless, to their dismay, the atmospheric oxygen disappeared at rates much faster than predicted and could not be maintained stably. So low was the oxygen in the enclosure's atmosphere that the crew members could not work inside even for short periods of time, and many of the plants and animals died.

- Can you form a hypothesis as to why oxygen levels in the sealed enclosure could not be maintained in Biosphere 2? (*Hint:* Scientists did not consider microbial activities in the soils!)
- How could you test this hypothesis?
- Can you suggest a potential solution to maintain oxygen concentrations in Biosphere 2?

What Is a Microbe?

LEARNING OUTCOMES:

- Explain why it is difficult to define what a microbe is.
- List exceptions to the definition that "microbes are so small that they are only visible under the microscope."

Traditionally, the term "microbe" describes free-living organisms so small (usually less than about 100 micrometers [μm]) that they are only visible under the microscope (hence, they are *microscopic*). There are exceptions to the general rule, and the size range for known microbes is quite broad (Fig. 1.1). Most microbes are too small to be seen without a microscope. For example, the bacterium *Escherichia coli* has a width of 0.5 μm and can reach 2 μm in length, a scale typical of many other microbes. On the lowest end of the size range are marine bacteria so minuscule (around 0.2 μm in diameter) that they are smaller than the largest viruses. Other microbes are so large that you can see them with the naked eye. *Epulopiscium fishelsoni* cells, for example, can grow

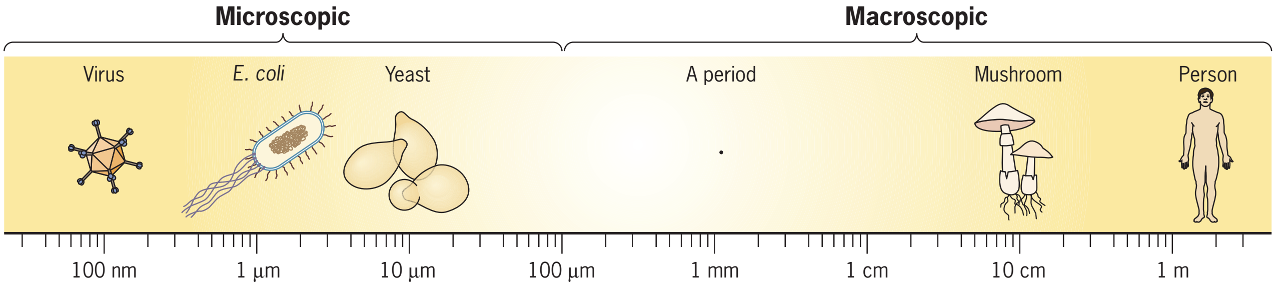


FIGURE 1.1 **Size range of microbes.** Microbes have a wide range of sizes, but most maintain a relatively small size. Typically, the human eye can detect objects of ~0.1 mm in size.

as big as the period at the end of this sentence. While many microbes are free-living organisms, there are exceptions; some exist in association with hosts. *E. fishelsoni* lives in the gut of surgeonfish. Some microbes take host dependency to the extreme by living *inside* host cells. This is the lifestyle of **obligate intracellular parasites**, such as the bacterium that causes leprosy (*Mycobacterium leprae*). Microbes have acquired myriad tricks to thrive in new niches, whether outside or inside hosts.

What about viruses? Although they can be as big as the smallest bacteria (Fig. 1.1), viruses are not considered to be microbes. Indeed, they lack one key quality of living cells: **the capacity to maintain their structural integrity throughout their life cycle**. To reproduce and mutate, viruses actually come apart during their reproductive cycle. Like cellular organisms, viruses are highly organized collections of nucleic acids and proteins. But these constituents are made separately and then assembled inside their host cells. Without the host cell, viruses could not produce progeny viral particles. In fact, viruses do not have the capacity to make proteins: they have no ribosomes, the protein factories of all cells. Instead, viruses rely on the host to supply the building blocks needed for biosynthesis of their macromolecules. Outside a host cell, a viral particle is inert and incapable of growth and reproduction. Despite not being microbes themselves, viruses do interact with microbial cells and are critical to their evolution. Viral biology is discussed in chapter 17.

What Do Microbes Look Like Under the Microscope?

LEARNING OUTCOMES:

- Compare and contrast the general structure of *Bacteria*, *Archaea*, and eukaryotic microbes.

Microbes have diversified to have many shapes: spheres (cocci), rods (bacilli), ovals, bowling pins, spirals, comma shapes, and even corkscrews (Fig. 1.2). You can appreciate the diversity of microbial shapes by examining a drop of pond water with a microscope (Fig. 1.3). Why so many shapes? Shape affects the efficiency of nutrient uptake, motility, attachment to surfaces, and even reproduction. As you examine them with a microscope, you will also realize that not all microbes are unicellular. Some form pairs, chains, or filaments or aggregate in some other unique pattern. In fact, in their natural environment,

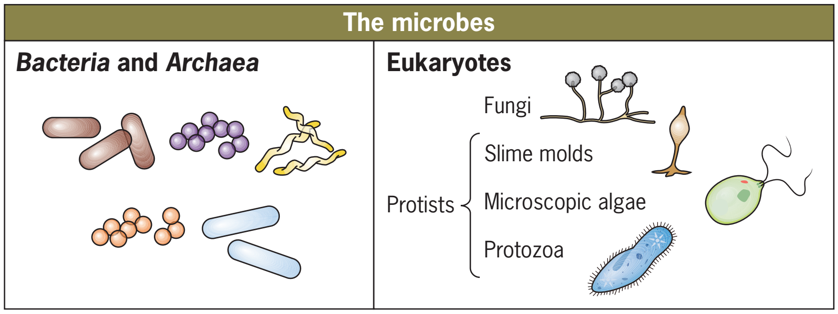


FIGURE 1.2 Microbes. Microbes—*Bacteria*, *Archaea*, and eukaryotes—come in many different shapes.

many microbes adhere to surfaces and form sophisticated three-dimensional communities, or **biofilms**, that come close to rivaling the complexity of our own tissues. In chapter 21, we will learn about microbe-microbe interactions, multicellularity, and the consequences of these social behaviors.

Microscopes also reveal a diversity of internal structures within microbial cells (Fig. 1.4). The most notable distinction is the absence of a nucleus in *Bacteria* and *Archaea* and its presence in eukaryotes. *Bacteria* and *Archaea* are two separate but very large and diverse groups. The body plan of the two is similar: in addition to lacking nuclei, they do not have membrane-bound organelles such as mitochondria or plastids. And yet, although they appear similar in size and morphology under the microscope, *Bacteria* and *Archaea* followed distinct evolutionary paths that led to unique defining features.

Sizes and morphologies are even more variable among the eukaryotic microbes, which include algae, fungi, and a diverse group of organisms collectively called the protists. Some of these groups are especially hard to delineate, in part because they have both small and large relatives. For example, yeasts are certainly microbes, but mushrooms are not, yet both are fungi. The same goes for algae—some are microscopic, others are the giant seaweeds (kelp). Still, they all follow the general cell body plan of having a true nucleus and most also have membrane-bound organelles.

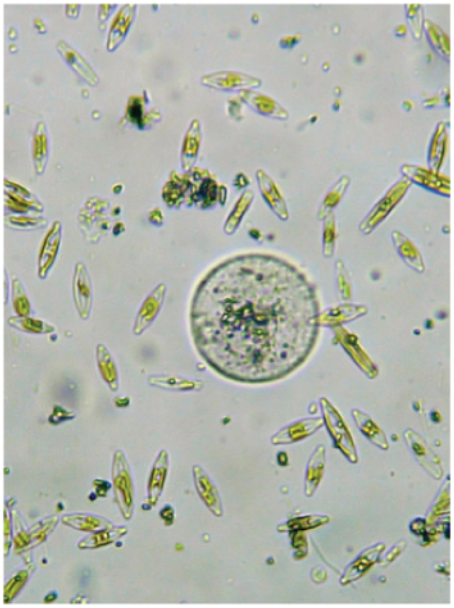


FIGURE 1.3 **Microbes' diverse shapes and forms.** A drop of pond water scum examined at ×400 magnification with a phase-contrast microscope reveals many different types of microbial cells. Photo courtesy of Daniel Jasso-Selles.

Does Size Really Matter?

LEARNING OUTCOMES:

- Describe some benefits and detriments to a microbe having a relatively small size.
- Explain why surface area-to-volume ratio is an important constraint in bacterial growth.

Throughout billions of years of evolution, microbes have diversified in many ways, but most have maintained a relatively small size. There is a key advantage to being small: their high surface-to-volume ratio maximizes chemical exchange with the surrounding environment. Cell volume is another way to

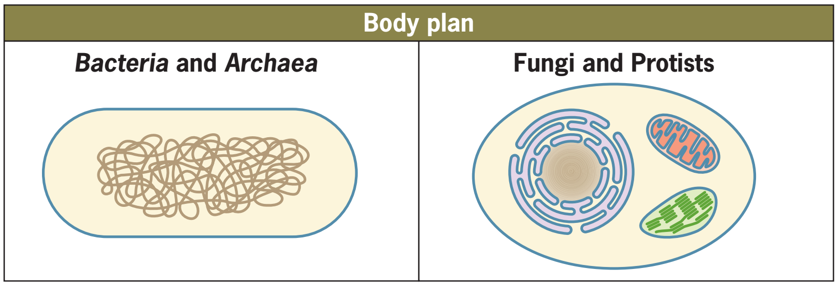


FIGURE 1.4 **Traditional classification of microbes as *Bacteria* and *Archaea*, or eukaryotes.** The classification depends on whether the cells lack (*Bacteria* and *Archaea*) or have (eukaryotes) a true nucleus. The eukaryotes also have membrane-bound organelles of bacterial ancestry: mitochondria and plastids.

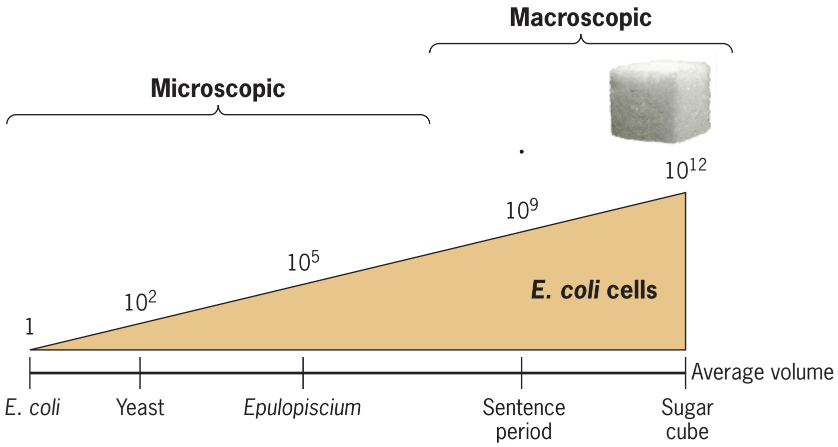


FIGURE 1.5 **Numbers, large and small, matter.** One billion of an average-sized bacterium such as *E. coli* occupy a volume comparable to the period at the end of this sentence. A sugar cube could accommodate a trillion of them! Larger microbes can also house bacteria inside and start amazing cooperative behaviors.

envision how small microbes really are (Fig. 1.5). The volume of a representative bacterium such as *E. coli* is about 1 μm^3, or roughly 1/1,000 that of a human cell. Eukaryotic microbes tend to be larger. For example, the baker's yeast, the eukaryotic microbe that is used to make bread, beer, and wine, has an average volume of around 100 μm^3, or 1/10 that of a human cell. That means it would take approximately 10^{17} bacteria or 10^{15} yeast cells to occupy the same volume as an adult human! If an *E. coli* cell were the size of a human being, a yeast cell would be as large as an elephant.

As cells grow larger, the volume increases more rapidly relative to the surface area and the rates of chemical exchange (**nutrients** diffusing in and waste products diffusing out) decrease proportionally. To keep their metabolism functioning at the highest possible rate to support rapid growth and reproduction, cells must exchange chemicals efficiently with their surroundings. Thus, rapidly growing microbes process their nutrients at rates 10 to 1,000 times higher per gram than do mammalian cells. Hence, even relatively small increases in size can make a big difference in chemical diffusion and, potentially, in cell growth (Box 1.1).

Rapid chemical turnover has significant consequences. One can get sick with a bacterial infection very quickly because bacteria grow to high numbers before our immune system can eliminate the threat. Fruits, vegetables, and meats more readily spoil outside the fridge because of the rapid growth and activities of microbes. And how long does it take for yeasts to grow and make bread rise? Hours!

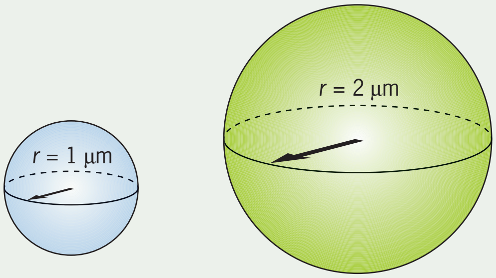
A high surface-to-volume ratio is particularly important in an environment where competition for nutrients is high. Some of the smallest known microbes live in marine and freshwater environments. The smallest on record, "*Candidatus* Actinomarina minuta," has an average cell volume of about 0.013 μm^3—60 times smaller than *E. coli*! Although this tiny bacterium has not been cultured, its genome has been sequenced directly from cells in the environment. With this information, scientists made probes specific to one of its ribosomal RNAs

BOX 1.1

Size Matters!

This activity illustrates how much cell size matters. Imagine two spherical cells, one with a radius of 1 µm and the other of 2 µm. If you were to examine the two cells under a microscope, they would still be tiny, right? Now let us calculate the surface-to-volume ratio with formulas shown in the figure. Note that the surface area increases as the *square* of its radius, but the volume increases as the *cube* of the radius.

- Did you come up with the surface/volume ratio of the two cells?
- Which one do you predict will grow faster?



Surface area ($4\pi r^2$)	12.6 µm^2	50.3 µm^2
Volume ($4/3\pi r^3$)	4.2 µm^3	33.5 µm^3
Surface/Volume	**3**	**1.5**

(16S rRNA) and used them to tag the cells and assess their abundance in seawater samples. The ultra-small bacterium is extraordinarily abundant in oceans around the world, representing ~4% of all the bacterioplankton. Its minute size pays off!

So why are some microbes large? Do they compromise their growth efficiency for size? Some compensate for their large volume by extending their surface area with membranous projections, so they can continue to grow quickly. Consider *E. fishelsoni*, the gargantuan bacterium of the surgeonfish's gut. As the *E. fishelsoni* cells grow larger, their membranes wrinkle, forming folds and pockets. This increases the surface area of the cell to maximize nutrient uptake and growth when the fish is actively feeding during the day. Once the fish stops feeding, the large *E. fishelsoni* cells reproduce by cycles of cell division. The next day, the progeny are ready to start feeding, repeating the cycle of growth once again.

Being small also has some disadvantages. Small microbes are an easy target for larger microbes and animals (e.g., whales feeding on plankton in the oceans). Some microbes avoid getting eaten by forming larger aggregates, sometimes with other microbes. Such masses of cells are often visible to the naked eye and to a predator, and together they are not so easy to digest.

How Many Microbes Are on Earth? On Your Body?

LEARNING OUTCOMES:

- Consider why the immensity of the microbial world was unknown until the very end of the early 20th century.

Small as individual microbes are, their total collective mass on Earth is staggering. Microbes are ubiquitous, and they are found practically anywhere there is free liquid water. In the oceans alone, microbes account for more than 90% of the biomass. There are nearly 1 million bacterial cells in 1 ml (approximately 20 drops) of seawater, a total of about 10^{30} cells in all the world's oceans. And these numbers are just for bacteria. Archaea are also abundant there. Plus, eukaryotic microbes account for almost half of the microbial biomass in the ocean's surface waters. Microbes are even more abundant in soils, sediments, and regions below the two (the subsurface). Collectively, the microbial biomass on the planet is at least as much as all other living things on the planet. The immensity of the microbial world was not known until the very end of the 20th century. Their importance to Earth's health is clear: Because they contain proportionally more nitrogen and phosphorus than plants, bacteria and archaea are the largest reservoir of these essential elements in the biological world. In chapter 19, we will learn more about the contribution of microbes to the cycling of these and other elements.

Numbers, large and small, matter. A trillion of your average-sized bacterium weigh scarcely a gram and occupy a volume approximately that of a sugar cube (Fig. 1.5). Yet some diseases, such as bacterial dysentery, are acquired by swallowing just a few bacterial cells. For these microbes, the number of cells contained in the sugar cube is sufficient to infect not only all humans but also all other susceptible vertebrates on Earth, with plenty to spare. How much fecal contamination would it take to pollute a large body of water and make even a few swallows of its water infectious? Not much, probably less than the bacteria you could fit in the sugar cube. And our bodies contain more bacteria than human cells, though, collectively, the bacteria occupy a very small volume. The lower intestines alone house a kilogram or two of microbes, accounting for almost one-half of the dry weight of our feces. Such crowding is not unusual in nature. As we mentioned earlier, microbes preferentially associate with surfaces, where they build biofilms. All types of surfaces are colonized, from a rock to your intestine. The space between teeth and gums contains wall-to-wall bacteria—no wonder dental hygienists probe the gingival crevice for pockets! Microbes may be small, but they are present in great numbers.

How Long Have Microbes Been on Earth?

LEARNING OUTCOMES:

- State three characteristics of LUCA, the last universal common ancestor.
- Explain how the three-domain tree is different from the "ring of life" model.
- Describe the impact cyanobacteria had on early Earth.

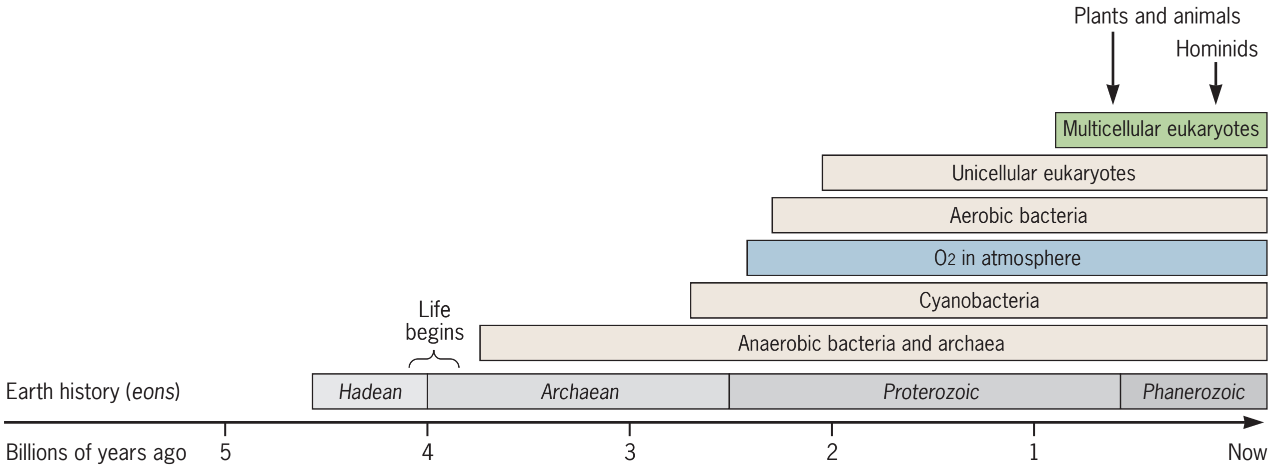


FIGURE 1.6 **Evolution of life forms on Earth.** *Bacteria* and *Archaea* branched early on after life began some 4 billion years ago. Microbial life was anaerobic until the emergence of cyanobacteria, which carried out a type of photosynthesis (oxygenic) that produced oxygen (O_2) as a by-product. This critical event oxygenated the planet and the atmosphere and provided the planetary conditions for the evolution of aerobic bacteria and then eukaryotic microbes. Microbial life dominated the planet for about the first 3 billion years, until the first multicellular eukaryotes emerged. The current eon, the Phanerozoic, is the shortest of all (542 million years), yet includes the eras when relatively simple animals and plants arose: the Paleozoic era (542 million to 248 million years ago); the age of dinosaurs, birds, and fish (Mesozoic era; 248 million to 65 million years ago); and the era of mammals (Cenozoic era; 65 million years ago until now).

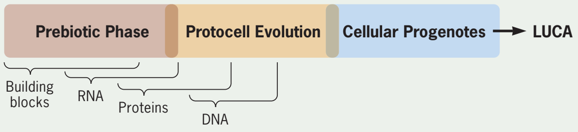
The staggering abundance of microbes is the direct result of their long evolutionary path (Fig. 1.6). *Bacteria* and *Archaea* branched early on from a common ancestor; from them, all other life forms originated. Just how LUCA originated is anybody's guess (Box 1.2). Evidence of our shared ancestry is the fact

BOX 1.2

Who Is "LUCA"?

We really don't know, but that has not prevented scientists from speculating about its cellular features and origin. Scientists agree that the last universal common ancestor, or LUCA, had the cellular features that are universal to extant organisms:

- DNA as genetic material
- Proteins and RNAs to catalyze essential processes needed to grow and reproduce
- A lipid membrane to enclose all its components



Before LUCA was formed, there was a prebiotic phase in the hot, early Earth when life's essential building blocks and molecules were generated in spontaneous chemical reactions. A popular theory suggests that RNAs came first, and they were able to self-replicate and catalyze chemical reactions. At some point the RNAs were engulfed in lipid micelles to make primitive cellular entities, or **protocells**. The protocells also evolved: the RNAs evolved the ability to make proteins from amino acids, and the primitive metabolisms were born. Proteins also catalyzed the synthesis of the first DNA molecules using RNA templates. At this time in life's history there may have been large populations of cellular progenitors containing DNA, RNA, and proteins. They were presumably promiscuous, exchanging a lot of their genetic material via horizontal gene transfer, thereby diversifying rapidly. From this population only one cell, LUCA, reproduced so successfully that it outcompeted the rest. And it is from this common ancestor that all living forms, including us, originated.

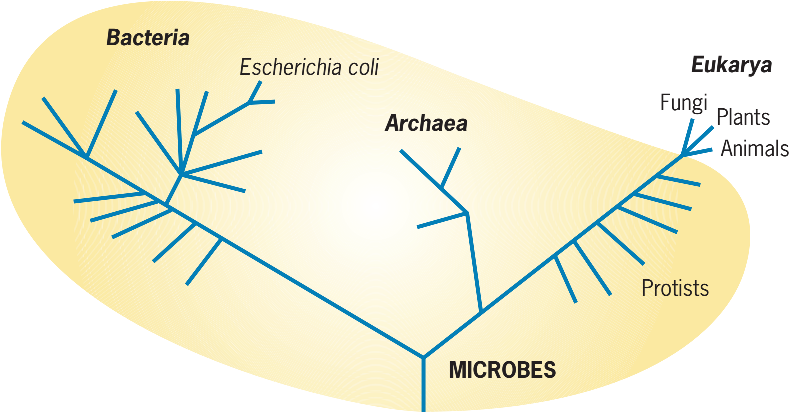


FIGURE 1.7 **Simplified representation of the classical three-domain tree.** The *Bacteria* and *Archaea* domains branched first, and the *Eukarya* (eukaryotes) branched out from the *Archaea*. Each domain is subdivided into a number of phyla (small branches in the tree). Note that there are microbes in the three domains and that they contribute far more phyla than the macroscopic organisms. Animals, plants, and fungi are actually perched on a small branch of this "tree of life."

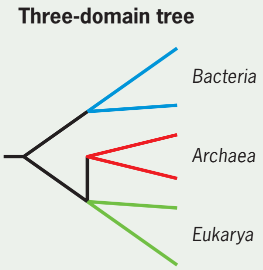
that all extant organisms, including humans, contain footprints of a unique ancestor in their DNA, much as our DNA contains information from our parents, grandparents, and all the generations that preceded them. The most useful DNA sequences to reconstruct the evolution of life on Earth are those encoding processes shared by all extant life forms, such as ribosome-mediated protein synthesis. Carl Woese examined the relatedness of the small rRNA genes of different organisms and recorded the number of mutations that accumulated in these genes. From this information he deduced the evolutionary history, or **phylogeny**, of various microbial and nonmicrobial organisms (Fig. 1.7). The tree showed three distinct evolutionary groups or domains (*Bacteria*, *Archaea*, and *Eukarya*), each appearing as branches of a tree trunk rooted in a common ancestor. Looking at the tree, it is easy to appreciate that the branch point of *Bacteria* and *Archaea* descent is ancient; furthermore, the *Eukarya* domain evolved from an ancestral archaeon before the archaeal lineage diversified.

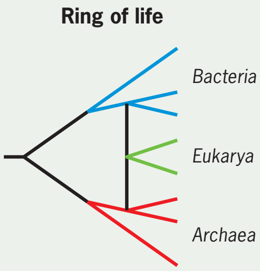
Since Woese's pioneering phylogenetic studies, the genealogy of all life forms was reconstructed using many other genes and their accumulation of mutations. All of these analyses supported the three-domain view, with the early branching of *Bacteria* and *Archaea* and then branching of *Eukarya* from the *Archaea* lineage. To some scientists, this phylogenetic tree helped explain why some archaeal processes such as DNA replication and transcription (to make RNAs) are more similar to the eukaryotic ones than to those of the *Bacteria*. However, the validity of the three-domain scheme has been challenged by improved and more accurate phylogenetic methods. In an era when entire genomes can be sequenced inexpensively and rapidly, even from organisms that are not available in pure culture, researchers have turned to analyzing whole genomes rather than genealogy-specific genes such as rRNA. To study the relatedness of organisms, these analyses not only rely on mutational changes of genes but also consider another major driver of variation: horizontal gene transfer (i.e., the lateral exchange of genetic material among organisms). Such phylogenetic studies no longer support the three-domain phylogeny. Rather, genome-scale data support a "ring of life" model in which the *Eukarya* are no longer a primary lineage of life but a chimeric group of symbiotic origin from the *Bacteria* and *Archaea* lineages (Box 1.3).

BOX 1.3

A Three-Domain Tree or a Ring of Life?

Horizontal gene transfer (i.e., the lateral movement of one or more genes from one organism to another) is an important source of genetic variation among organisms. In fact, rRNAs can be transferred this way as well. Hence, mutational changes in rRNAs, as used to measure relatedness in the iconic three-domain tree, provide only a partial glimpse of the evolutionary past of all organisms. This limitation is bypassed by genome-scale analyses that have revealed three different evolutionary features of eukaryotes:


Three-domain tree


Ring of life

- Some eukaryotic genes are related to cyanobacteria, consistent with the symbiotic origin of eukaryotic photosynthetic organelles (such as chloroplasts) from a cyanobacterial ancestor.
- Another set of eukaryotic genes is closer to the bacterial group *Alphaproteobacteria*, consistent with the symbiotic origin of the eukaryotic mitochondrion from an ancestral alpha-type bacterium.
- One other set of genes places the eukaryotes within the *Archaea* domain, consistent with the acquisition of mitochondria and/or chloroplasts by an ancestral archaeal host cell.

The "ring of life" tree reconciles the genomic data by placing the *Bacteria* and *Archaea* as the two primary and ancient lineages evolved from a common ancestor. The eukaryotes are no longer a separate domain, but a hybrid group evolved from the *Bacteria* and *Archaea* groups after their diversification had already begun.

Regardless of the phylogenetic approach, all trees reveal the enormous phylogenetic diversity of the microbial lineages, particularly the *Bacteria* and *Archaea* groups. This should not surprise us: *Bacteria* and *Archaea* had the planet to themselves for nearly 2 billion years and diversified their metabolisms to adapt to the myriad planetary changes they encountered along the way (Fig. 1.6). In the process, they transformed Earth into the planet that we know today. First to evolve were anaerobic metabolisms, which thrived in the oxygen-free early Earth. But once cyanobacteria arose almost 3 billion years ago, they carried out a new form of photosynthesis that released oxygen as a by-product. The ancestral cyanobacteria produced so much oxygen that they oxygenated the planet surface and its atmosphere. Let us pause here to discuss the impacts of releasing so much oxygen: the greenhouse gas methane was oxidized and global temperatures plummeted. The extreme cold triggered the first glaciation, covering the planet with its first blanket of snow! This deep freeze killed many of the early microbes and selected for those adapted to the cold. Meanwhile, the abundant oxygen killed many of the early anaerobic microbes but also exerted selective pressure for the evolution of oxygen-tolerant microbes and aerobic bacteria. The latter grew abundantly by respiring the abundant O_2. The first unicellular eukaryotes emerged when an archaeal cell "ingested" an aerobic bacterium, prey that became the energy factory of eukaryotic cells: the mitochondrion.

By the time the first multicellular eukaryotes appeared some 750 million years ago (Fig. 1.6), microbes had been the planet's only inhabitants for more than 3 billion years! Why is that? Microbes are the only forms of life that are self-sufficient; that is, only they can exist indefinitely without any other living things. They can also mutate, exchange genetic material, and reproduce rapidly, creating opportunities to diversify their metabolisms and adapt to the changing environment. Along the way, microbes transformed Earth and left numerous footprints of their past activities. It may be hard to believe, but some chemicals made by these ancient microbes have survived in the rocks to this day. These microbial products are useful biomarkers that tell scientists what microbes once lived there and what they were doing! In some cases, the microbes themselves have been preserved in the rocks in mineralized form (microfossils). Together, the molecular (DNA footprints) and the geological (mineral footprints) records enable scientists to reconstruct chapters of the history of microbes on Earth with outstanding precision. Amazing!

Are Microbes Everywhere on Earth?

LEARNING OUTCOMES:

- Give examples of how metabolism dictates where an organism can grow.
- Justify the following statement: "No niche on Earth that supports life is without microbes."

It is not surprising that every niche on Earth that supports life contains microbes. This includes environments considered extraordinarily harsh. Credibility is strained here: microbes not only survive but actually grow under extreme conditions, such as temperatures above that of boiling water, very acidic pH, pressures of thousands of atmospheres, and the salinity of concentrated brine (Table 1.3). The current world champion among **thermophiles** (as organisms that grow only at high temperatures are called) is strain 121, an archaeon that grows at (yes, you guessed it) 121°C! Moreover, this champion can survive for several hours at 130°C. Such temperatures are only attainable at high pressures, such as those found in deep-sea hydrothermal vents. To grow such an organism in the laboratory requires a pressure cooker or an autoclave. Even though laboratories routinely use autoclaves to sterilize microbiological media, not only do their high heat and pressure fail to kill this heat-loving microbe, but these extreme conditions support its growth. Equally amazing are microbes that grow and survive under extremes of pH or salinity that would immediately kill most other cells. Clearly, we have an anthropocentric view of life: we think that

TABLE 1.3 The known extremes of life

Some microbes *survive*:
- Very high temperatures (up to 130°C)
- 5 megarads of gamma radiation (ca. 10,000 times what would kill a human)
- Very high pressures (ca. 8,000 atmospheres, or 117,000 pounds per square inch)

Some microbes *grow at*:
- Extremes of pH (0 to 11.4)
- Extreme temperatures (–15 to 121°C)
- High hydrostatic pressures (ca. 1,300 atmospheres, or 18,500 pounds per square inch)
- High osmotic pressures (5.2 M NaCl)

these organisms are bizarre, and we call them **extremophiles**. However, from the perspective of these organisms, a temperature of 37°C, a pH of 7, and low salinity are not simply uncomfortable but are actually incompatible with life.

Microbes have also diversified their metabolisms to use a narrow or a wide range of nutrients. The "picky eaters" can only utilize a narrow spectrum of carbon and energy sources, restricting themselves to environments where those particular nutrients are available. Many of the bacteria associated with the human body fall into this category, possibly because they have adapted to a rich and relatively constant environment. Other microbes utilize a wide range of substrates and can thrive in many environments. For example, certain species of *Pseudomonas* bacteria can metabolize hundreds of organic compounds; not surprisingly, they are abundant in soil, plant roots, bodies of water, and animals. At the other extreme are microbes adapted to environments with few or no organic nutrients. They may be limited to a minimal diet, but they live in environments without competitors. It is a trade-off. Many of the microbes on this planet are photosynthetic; in fact, they invented photosynthesis billions of years ago (Fig. 1.6). All they need is light to energize their metabolisms and atmospheric CO_2 to build their biomass, just like plants. Not surprisingly, these microbes (**phototrophs**) can colonize nutrient-poor environments, such as the surface waters of some lakes and oceans, as long as light is abundant. Other microbes have evolved ways to "extract" the energy not from light but from chemical reactions involving some intractable-sounding but energy-rich compounds. Imagine subsisting on hydrogen and iron or sulfides? For many microbes, that is a "normal" diet. As they do not rely on the energy of the sun to grow, you can find these microbes in dark places such as deep-sea hydrothermal vents in the ocean and in cracks and fissures in rocks. So large are these communities that, collectively, they are thought to outweigh all the oxygen-using organisms above ground. The extraordinary metabolic and ecological repertoire of such microbes has led to speculation that analogous life forms may even exist or have existed in other places in our solar system, including Europa, one of Jupiter's moons, and Mars (see Microbiologist at Work).

Each of these examples illustrates that microbes have diversified their metabolisms to occupy every planetary niche and to use any available resources. And the diversification continues to this day. New compounds are released into the environment through our industrial activities, yet even the most contaminated sites harbor numerous microbes. It has been said that for nearly any naturally occurring organic compound there is at least one kind of microbe that can break it down, as long as water is available. Indeed, microbes have been harnessed to clean up environmental pollution such as oil spills, a technique known as **bioremediation**. Given the immense metabolic versatility and the widespread presence of microbes, do you think life could originate anew? Or would the chemicals needed to make a cell be consumed by present-day environmental microbes before a new cell could be assembled from scratch?

Microbiologist at Work

The search for life on Mars entered an exciting new phase on February 21, 2021, when NASA's robotic explorer *Perseverance* landed on the red planet. To probe for chemical evidence of ancient microbial life, the rover is equipped to collect soil and core samples for its sophisticated UV spectrometer to examine for "buried treasure": organic compounds left behind by ancient microbes. To do so, NASA expertly directed *Perseverance* to a region of Mars that once had liquid water, nutrients, and other energy sources. To commemorate this historic achievement, the rover's touchdown site was named Octavia E. Butler Landing, honoring the African American science fiction writer. In addition to winning both the Hugo Award and the Nebula Award from the Science Fiction and Fantasy Writers of America, she was the first science fiction writer to earn a MacArthur Fellowship, a "Genius Grant" to promote exceptionally talented people working to address challenging global problems. NASA recognized that, like *Perseverance*, Octavia Butler's characters "embody determination and inventiveness," and her stories explore timeless themes of race, gender, equality, and humanity that continue to inspire "a bolder, more equitable future for all." Follow NASA's *Perseverance* mission at https://www.nasa.gov/perseverance.

Perseverence image courtesy of NASA/JPL-Caltech/University of Arizona, https://mars.nasa.gov/resources/25701/welcome-to-octavia-e-butler-landing/. Octavia Butler image courtesy of Nikolas Coukouma, under license CC BY-SA 2.5.

How Do Microbes Help Make a Planet Habitable?

LEARNING OUTCOMES:

- State two ways in which microbes directly impact your life.
- Describe three locations where microbes live that are surprising to you.

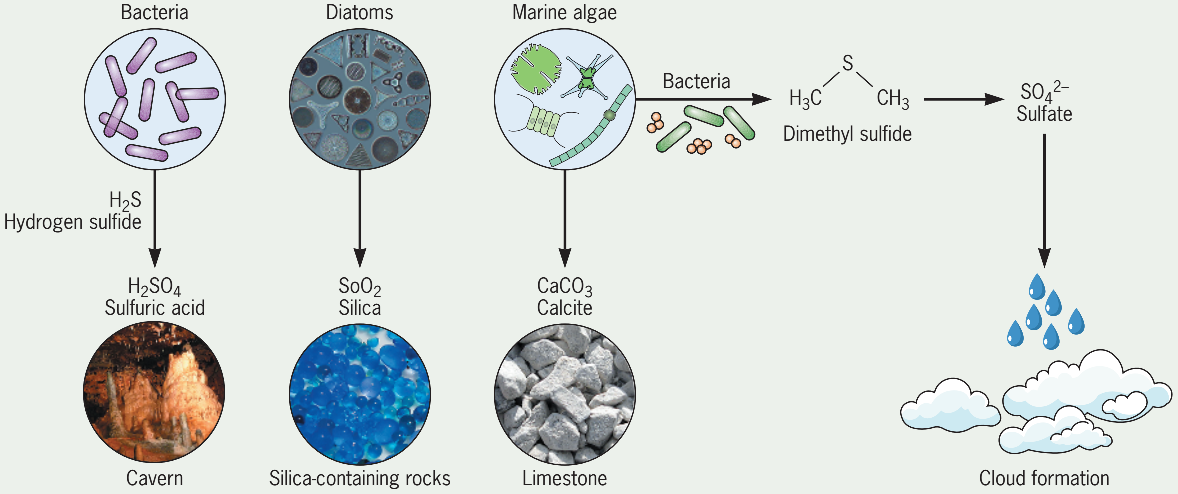
Taking into account the metabolic versatility of microbes, it should not require a leap of faith to realize that they play a major role in a variety of global processes (see Microbes at Work). How do microbes do this? Microbial communities link their metabolisms to carry out processes that they could never achieve individually, further expanding their metabolic potential. At a planetary scale, microbes carry out life-sustaining processes in the biosphere, including the

Microbes at Work

Diverse Microbial Metabolism

Microbes, acting alone or in consortia, impact the metabolism of several compounds that affect geology and the atmosphere.

In addition to the important work of recycling carbon, nitrogen, and oxygen, 4 billion years of evolution have led to the remarkable ability of some microbes to impact geological processes. For instance, many large caverns owe their existence to microbes that oxidize hydrogen sulfide to produce sulfuric acid, which solubilizes calcium carbonate. When this microbial acid comes into contact with water, it dissolves what was once rock! Other microbes *make* rocks by generating calcite, which is the main constituent of limestone. And diatoms account for huge deposits of silica-containing rocks. Other marine algae and bacteria combine forces to produce a volatile compound, dimethyl sulfide, that turns into sulfate in the atmosphere, acting as a nucleating agent for water vapor to become water droplets. The result? Clouds!



recycling of essential elements such as carbon, oxygen, and nitrogen. Let us consider oxygen once more: photosynthetic bacteria oxygenated our planet, and together with plants, they ensure that oxygen is constantly replenished to maintain stable levels in the modern atmosphere. Without it, all plants and animals and many microbes would not be able to respire and would die. Could cyanobacteria have helped scientists design a self-sustainable ecosystem in Biosphere 2 (see case above)?

And what about carbon? If microbes did not break down organic material, carbon would accumulate in dead plant matter, and there would not be enough carbon dioxide for plant growth. To cycle carbon and other elements, microbes also team up with nonmicrobial hosts. For example, mammals do not make enzymes that break down the cellulose in plant material. Instead, cattle, sheep, deer, and other ruminants harbor cellulose-digesting microbes in their **rumen**, essentially a large fermentation chamber. The animal provides the microbes with a suitable habitat for growth; the microbes reciprocate by breaking down the cellulose into volatile fatty acids, which the animal uses as a major energy source. Such interactions are part of the grand recycling system of all organic (carbon-containing) material on Earth. No animal or plant ever decomposes through the activities of a single microbial species. Food chains and interactive populations are the norm. Microbes also provide nitrogen for all living beings, thanks to their ability to fix this element from the atmosphere. Besides nitrates used for fertilizers, which are manufactured, *Bacteria* and *Archaea* are the only significant source of utilizable nitrogen, essential for all of life. If all bacteria went on strike and this microbial process ceased abruptly, plants would likely run out of usable nitrogen in about one week. Sometimes, not enough attention is paid to such microbial activities. The case study highlights this fact. (Have you figured out what microbial activities consumed O_2 in the enclosure's atmosphere so rapidly?)

CASE STUDY REVISITED: Where did the oxygen disappear to in the Biosphere 2 experiment?

Did you come up with a hypothesis about microbial activity as a sink for oxygen in Biosphere 2?

The scientists hypothesized that soil microbes were responsible for the disappearance of atmospheric oxygen in Biosphere 2. To test their hypothesis, they measured the organic content of the soils in the enclosure. The investigators soon realized that the soils in the enclosure had 2 to 5 times more compost and peat than regular soils. In other words, the microbes feasted on the copious organic matter in the soil and respired atmospheric oxygen in the process. So fast was their oxygen consumption that the plants could not keep up with the microbes: in 16 months, the atmospheric oxygen levels declined by half, and the flora and fauna began to die. As a last resort, the organizers started pumping oxygen in from the outside. The exhibit was never self-sustained like our planet. This experimental closed ecosystem illustrates the impact of microbes on our environment and their essential role in making Earth habitable.

What could have been done differently? Perhaps the scientists could have reduced the compost in the soils to limit the food supply to the soil microbes. Alternatively, they could have included large ponds for photosynthetic microbes to grow. The activity by these important aquatic microbes contributes as much oxygen to Earth's atmosphere as the plants on land. Photosynthetic microbes should have satisfied the demands of the soil microbes and maintained stable levels of oxygen in the enclosure's atmosphere. After all, this is exactly what these microbes did when they emerged on Earth almost 3 billion years ago: they oxygenated the planet and gave us a breathable atmosphere!

Conclusions

Microbes are small, ubiquitous, abundant, adaptable, and necessary for the continued existence of other life forms. They were the first forms of life on our planet and are the ancestors of all organisms. The more we learn, the more evident it becomes that microbes play a vital role in shaping the planet and impacting human, animal, and environmental health. Indeed, the importance of the relationships between humans, animals, the environment, and microbes inspired the "One Health" initiative. Basic and social scientists and health professionals define One Health as "the collaborative effort of multiple disciplines—working locally, nationally, and globally—to attain optimal health for people, animals and the environment.” Fundamental to these efforts to attain optimal health are microbes! We now recognize that in terrestrial and aquatic ecosystems, human enterprises and agricultural and industrial activities alter microbial ecology. And since everything is interconnected, what affects our environment can then impact animals and humans. Although the One Heath initiative was originally motivated by concern over human practices that increase the risk of emergence of zoonotic infectious and noninfectious diseases, the paradigm now includes multiple pressing global issues, including climate change, food safety, food security, biodiversity protection, and the growing problem of antimicrobial resistance (Fig. 1.8). This is an especially pressing problem in bacteria that cause disease in humans. Of course, the genes encoding antibacterial resistance aren’t limited to just human pathogens. Antimicrobial resistance genes are mobile and promiscuous, passing through humans into animals and the environment, which serves as a reservoir of resistance determinants that can be picked up by other microbes, eventually finding their way into new hosts. We will discuss these at length in chapter 10. Throughout this book, we will frame fundamental concepts using a One Health approach to illustrate how the defining features of microorganisms—their physiology, genetics, ecology, and evolution—impact the overall health and wellness of our planet and all living creatures.

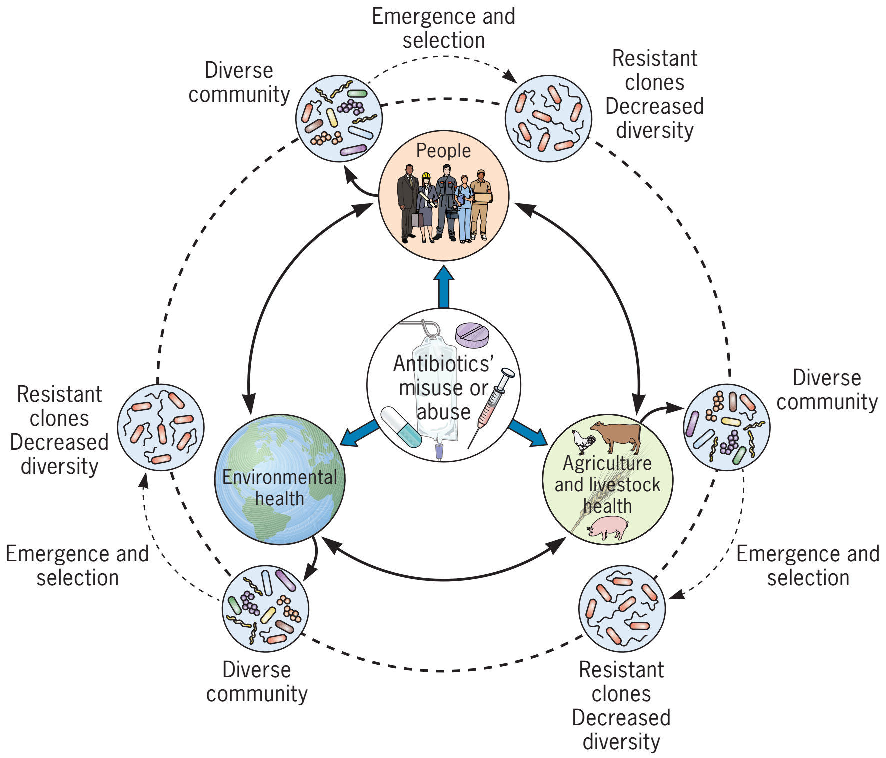


FIGURE 1.8 **Antimicrobial resistance and One Health.** The development of antimicrobial resistance involves the indiscriminate use of antimicrobials in humans, animals, and the environment, which facilitates the spread of resistant bacteria and resistance determinants around the world.

Supplemental Material

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Activities

BIG CONCEPTS REVIEW

For each of the ASM Fundamental Statements presented in the Key Concepts Box at the start of this chapter:

A. Associate the Fundamental Statements with each learning outcome at the beginning of every section.

B. Write responses to each learning outcome.

CHECK YOUR UNDERSTANDING

1. Why are viruses not considered microbes? (One or more answers possible)
   a. They are smaller than 1 μm.
   b. They do not remain intact during replication.
   c. They require host cells to grow.
   d. They lack nucleic acids to store genetic information.
   e. They must possess lipid membranes.
2. Bacteria range in volume over 1-million-fold. Discuss some of the consequences of being much larger or much smaller than the average *E. coli* cell.
3. The majority of microbial communities consist of hundreds or even thousands of species, all of which compete for available resources within any given ecosystem. Can you explain how so many microbial species can coexist, even as they compete for a common resource? Why aren't they outcompeted, leading to a less diverse community?