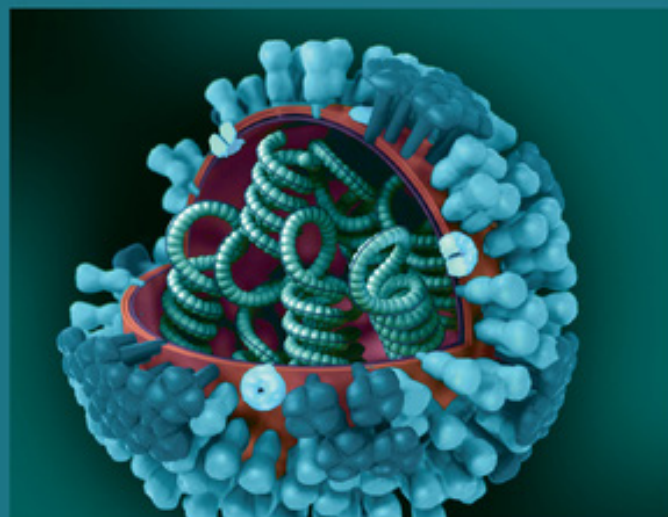


THIRD EDITION

Microbe



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To Fred Neidhardt and Elio Schaechter,
treasured colleagues, role models, and friends

—MSS

To curious and inquisitive learners everywhere

—EAJ

For my teachers in science, swimming, and yoga alike

—REAH

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Preface

Welcome to the third edition of *Microbe!* We've made every effort to write this book in an engaging and easy-to-understand style to communicate the fundamentals of microbial life, microbial diversity, microbial ecology, and pathogenesis with an eye toward increasing your comprehension and building your scientific confidence.

Throughout the text, we have adopted a One Health framework to highlight the interconnection between people, animals, plants, environment, and the diverse microbial world on Planet Earth. Each chapter is written to stimulate scientific thinking and encourage you to actively reflect on and apply the knowledge and skills that you are learning. As in previous editions, we begin every chapter with a set of key concepts and fundamental statements from the *ASM Curriculum Guidelines for Undergraduate Microbiology*. Case studies provide real-world applications about the way microbes are put together, what they must do to grow and survive, and how they interact with living things and the world around them. We further divide every chapter into sections, each with a set of learning outcomes to help guide your study and emphasize conceptual mastery over memorizing details.

Regarding nomenclature, after this text had gone to press, the International Committee on Systematics of Prokaryotes voted to rank phylum names under the rules of the International Code of Nomenclature of Prokaryotes. Organisms within this text retain their previous names, for the sake of clarity and consistency as the scientific community begins to process and implement this new nomenclature. For more information, instructors can refer to the online materials that accompany this text and Oren and Garrity, *Intl J Syst Evol Microbiol* 2021; 71:005056.

This edition of the book contains updated and visually compelling illustrations created by a skilled and educated artist to illuminate microbial processes in a clear and effective way. The field of microbiology contains a diversity of topics with an equally diverse scientific community driving the research. To celebrate this diversity, we have included new elements that feature microbiologists doing innovative and cutting-edge research and others that showcase the remarkable array of microbes and their fascinating capabilities. Each chapter concludes with updated references for further reading and a set of review and comprehension questions.

We have developed new robust instructor materials, including slides with figures and tables from the text and access to more than 250 peer-reviewed questions for undergraduate microbiology education. The accompanying instructors' manual features answers for end-of-chapter questions as well as supplemental active learning exercises and resources to challenge students to dig deeper into their understanding of the material. We hope this new *Microbe* edition stimulates your curiosity and excitement about the microbial world around you!

Acknowledgments

We are indebted to ASM Press for their generous support during the development and production of each edition of this book. Their staff and the freelancers who worked on this book provided the skills, expertise, and patience needed to turn our manuscripts and figures into a book. Christine Charlip (Director) led a terrific team consisting of our insightful and organized editor Megan Angelini and graphic artist Patrick Lane. Thank you all for your many insights and dedication to the project.

Special appreciation is extended to authors of the previous edition, Gemma Reguera, Moselio Schaechter, and Fred Neidhardt, whose insightful contributions to the second edition provided the foundation for this new edition. We also remain grateful for the many individuals who provided material for the Supplemental Activities first developed for the second edition of this text: Dr. Rachel Horak provided leadership to the authors and to graduate students Mike Manzella and Becky Steidl at Michigan State University and a team of postdocs at the University of Michigan comprised of Drs. Zack Abbott, Melissa Smaldino, Philip Smaldino, Laura Mike, Melody Zeng, Kalyani Pyaram, and Marc Sze. We are also grateful to Dr. Jamie Henzy for her virology expertise.

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About the Authors



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PART

Fundamentals of Microbial Life



IN THIS CHAPTER

Introduction

What is a microbe?

What do microbes look like under the microscope?

Does size really matter?

How many microbes are on Earth?

On your body?

How long have microbes been on Earth?

Are microbes everywhere on Earth?

How do microbes help make a planet habitable?

Conclusions

Supplemental material

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.

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

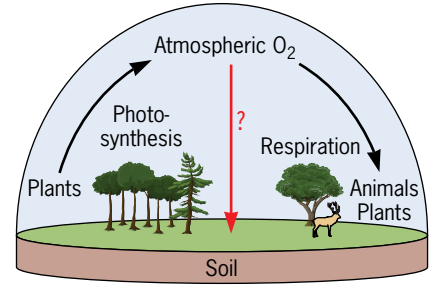
The source of all life forms
More phylogenetically diverse than plants and animals
Enormously abundant
Inhabit virtually every place on Earth where there is liquid water
Carry out transformations of matter essential for life
Transform the geosphere
Affect the climate
Participate in countless symbiotic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

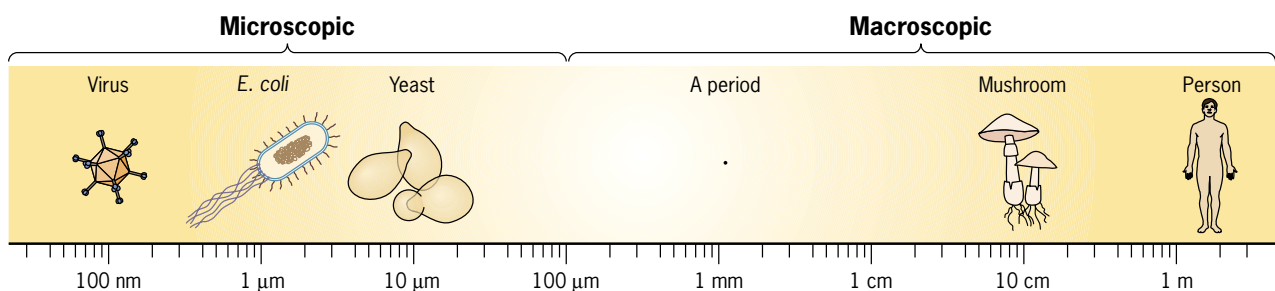


FIGURE 1.1 Size range of microbes. Microbes have a wide range of sizes, but most maintain a relatively small size. Typically, the human eye can detect objects of ~ 0.1 mm in size.

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.

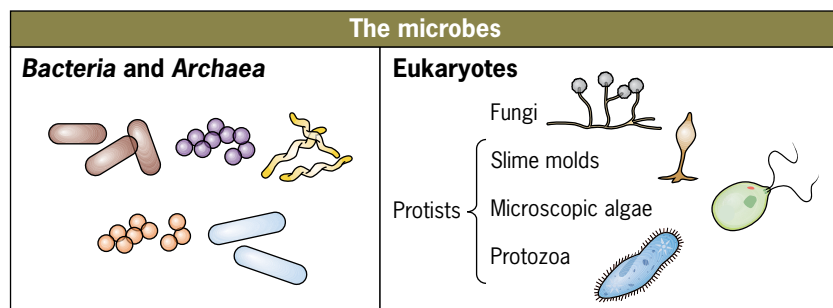
What Do Microbes Look Like Under the Microscope?

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.

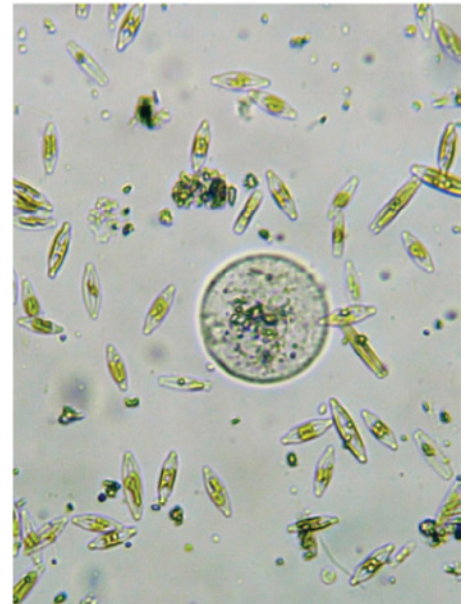


FIGURE 1.3 Microbes' diverse shapes and forms. A drop of pond water scum examined at $\times 400$ magnification with a phase-contrast microscope reveals many different types of microbial cells. Photo courtesy of Daniel Jasso-Selles.

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

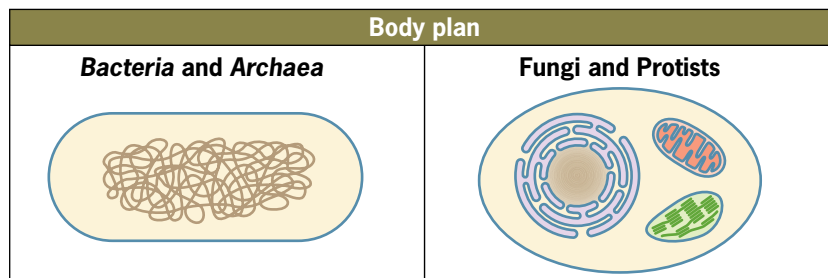


FIGURE 1.4 Traditional classification of microbes as *Bacteria* and *Archaea*, or eukaryotes. The classification depends on whether the cells lack (*Bacteria* and *Archaea*) or have (eukaryotes) a true nucleus. The eukaryotes also have membrane-bound organelles of bacterial ancestry: mitochondria and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

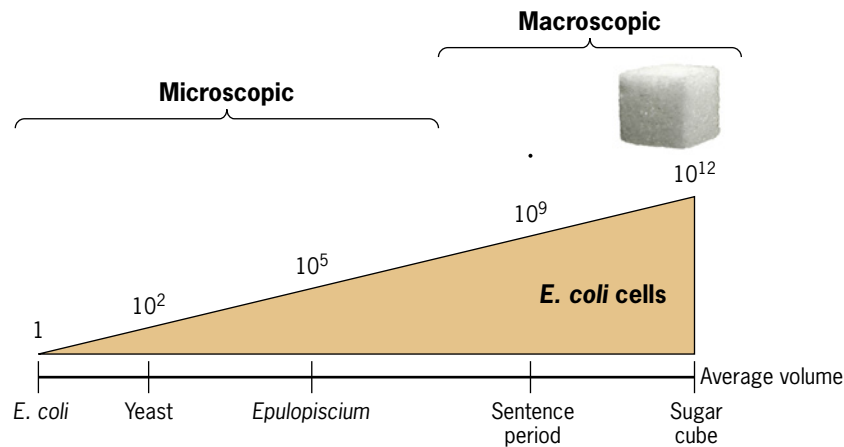


FIGURE 1.5 Numbers, large and small, matter. One billion of an average-sized bacterium such as *E. coli* occupy a volume comparable to the period at the end of this sentence. A sugar cube could accommodate a trillion of them! Larger microbes can also house bacteria inside and start amazing cooperative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

envison how small microbes really are (Fig. 1.5). The volume of a representative bacterium such as *E. coli* is about $1 \mu\text{m}^3$, 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 $100 \mu\text{m}^3$, 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 $0.013 \mu\text{m}^3$ —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

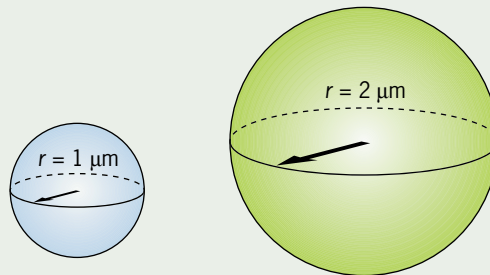
BOX 1.1

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.

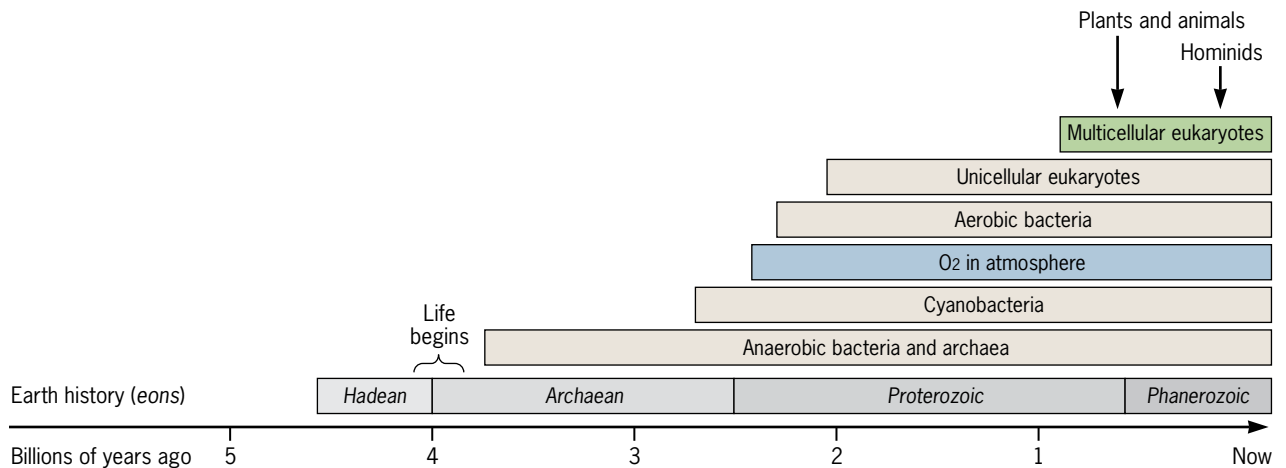


FIGURE 1.6 Evolution of life forms on Earth. *Bacteria* and *Archaea* branched early on after life began some 4 billion years ago. Microbial life was anaerobic until the emergence of cyanobacteria, which carried out a type of photosynthesis (oxygenic) that produced oxygen (O₂) as a by-product. This critical 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).

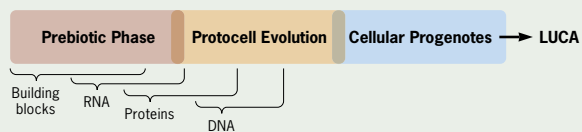
The staggering abundance of microbes is the direct result of their long evolutionary path (Fig. 1.6). *Bacteria* and *Archaea* branched early on from a common ancestor; from them, all other life forms originated. Just how LUCA originated is anybody's guess (Box 1.2). Evidence of our shared ancestry is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

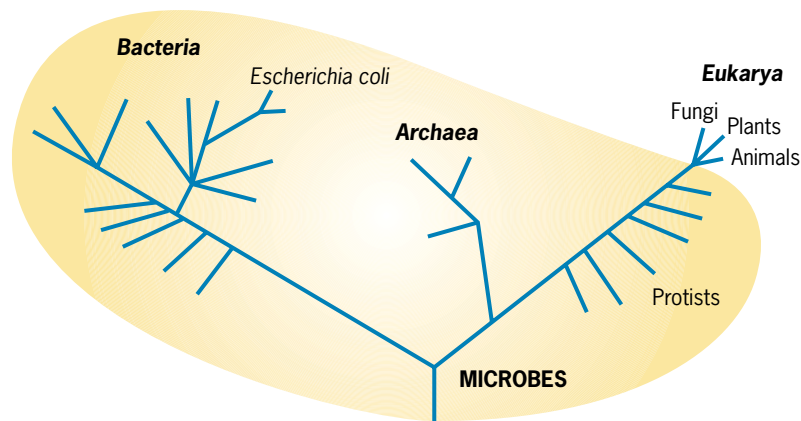


FIGURE 1.7 Simplified representation of the classical three-domain tree. The *Bacteria* and *Archaea* domains branched first, and the *Eukarya* (eukaryotes) branched out from the *Archaea*. Each domain is subdivided into a number of phyla (small branches in the tree). Note that there are microbes in 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.”

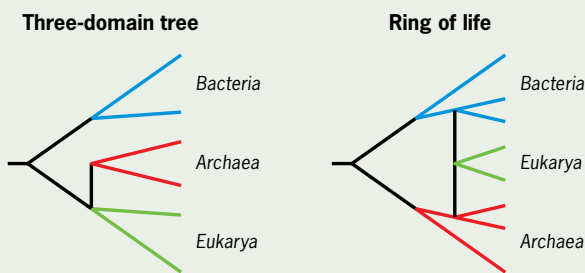
that all extant organisms, including humans, contain footprints of a unique ancestor in their DNA, much as our DNA contains information from our parents, grandparents, and all the generations that preceded them. The most useful DNA sequences to reconstruct the evolution of life on Earth are those encoding 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:



- 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 <i>survive</i> :
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 <i>grow at</i> :
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)
