FOURTEENTH EDITION

BROCK BIOLOGY OF MICROORGANISMS

MADIGAN • MARTINKO • BENDER • BUCKLEY • STAHL

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Brock Biology of Microorganisms is now available with MasteringMicrobiology!

MasteringMicrobiology is Pearson's online homework, tutorial, and assessment system designed to improve results by helping students quickly master concepts. Students benefit from self-paced tutorials that feature immediate wrong-answer feedback and hints that emulate the office-hour experience to help keep students on track.

Learning REVOLUTIONIZED

Up-to-Date Presentation

Reorganized and reimagined, the Fourteenth Edition of *Brock Biology of Microorganisms* provides the most up-to-date, accurate, and approachable introduction to the study of microbiology for today's students. Recognizing that mastering the principles of the dynamic field of microbiology today requires understanding the underlying molecular biology, the Fourteenth Edition provides both the foundation for the science and the science itself.

Brock Biology of Microorganisms guides students through the six major themes of microbiology in the 21st century as outlined by the American Society of Microbiology Conference on Undergraduate Education (ASMCUE): Evolution, Cell Structure and Function, Metabolic Pathways, Information Flow and Genetics, Microbial Systems, and The Impact of Microorganisms. Reflecting how the "omics" revolution has transformed all of biology, an undercurrent of genomics supports content in every chapter of the Fourteenth Edition.

New Dynamic Art

An enhanced and revised art program in the Fourteenth Edition provides the consistency and context students need to visualize microbiology. With new illustrations, significant art style updates, and nearly 200 new color photos, the Fourteenth Edition beautifully presents microbiology as the visual science it is today.

Consistent and Concise This new figure covers billions of years of evolution in a concise and effective manner. The appealing and engaging art program depicts biological elements consistently.

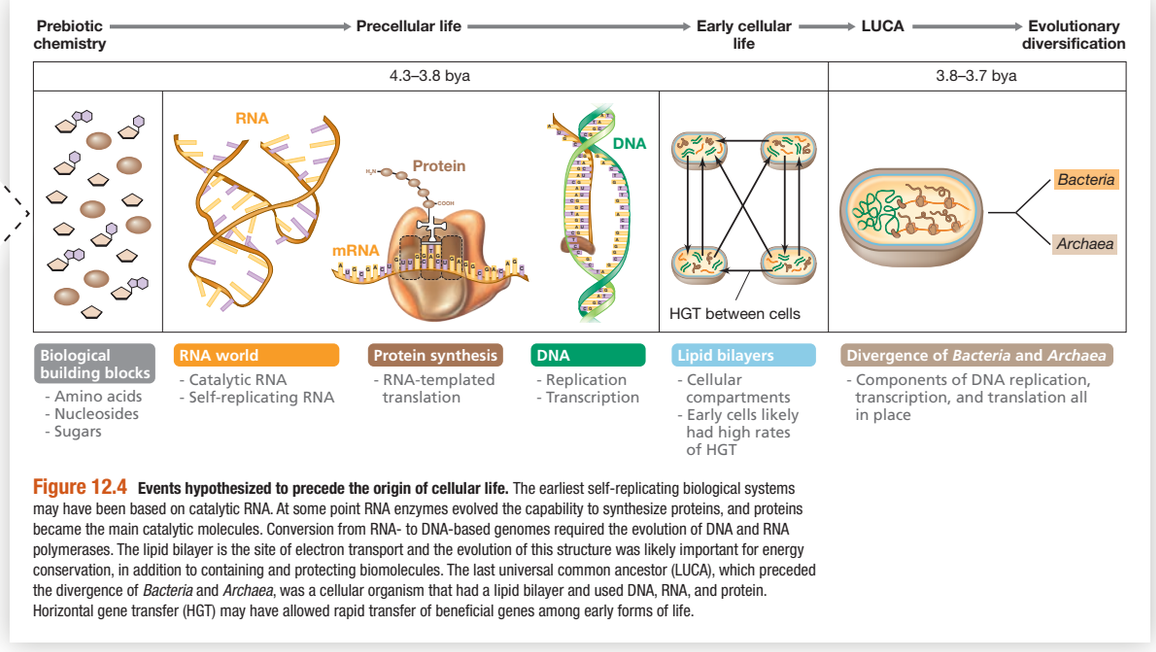

Figure 12.4 **Events hypothesized to precede the origin of cellular life.** The earliest self-replicating biological systems may have been based on catalytic RNA. At some point RNA enzymes evolved the capability to synthesize proteins, and proteins became the main catalytic molecules. Conversion from RNA- to DNA-based genomes required the evolution of DNA and RNA polymerases. The lipid bilayer is the site of electron transport and the evolution of this structure was likely important for energy conservation, in addition to containing and protecting biomolecules. The last universal common ancestor (LUCA), which preceded the divergence of *Bacteria* and *Archaea*, was a cellular organism that had a lipid bilayer and used DNA, RNA, and protein. Horizontal gene transfer (HGT) may have allowed rapid transfer of beneficial genes among early forms of life.

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BROCK BIOLOGY OF MICROORGANISMS

FOURTEENTH EDITION

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Credits can be found on page 961.

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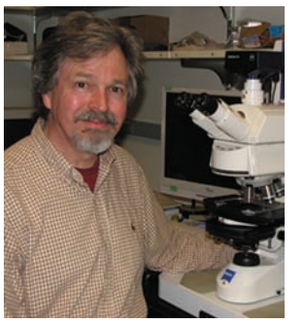
About the Authors

Michael T. Madigan received his B.S. in Biology and Education from Wisconsin State University–Stevens Point (1971) and his M.S. (1974) and Ph.D. (1976) in Bacteriology from the University of Wisconsin–Madison. His graduate research was on the hot spring bacterium *Chloroflexus* in the laboratory of Thomas Brock. Following three years as a postdoctoral scientist at Indiana University, Mike moved to Southern Illinois University Carbondale, where he taught courses in introductory microbiology and bacterial diversity as a professor of microbiology for 33 years. In 1988 Mike was selected as the Outstanding Teacher in the College of Science and in 1993, the Outstanding Researcher. In 2001 he received the SIUC Outstanding Scholar Award. In 2003 he received the Carski Award for Distinguished Undergraduate Teaching from the American Society for Microbiology, and he is an elected Fellow of the American Academy of Microbiology. Mike's research is focused on bacteria that inhabit extreme environments, and for the past 15 years he has studied Antarctic microbiology. In addition to research papers, he has edited a major treatise on phototrophic bacteria and served for 10 years as chief editor of the journal *Archives of Microbiology.* He currently serves on the editorial board of the journals *Environmental Microbiology* and *Antonie van Leeuwenhoek*. Mike's other interests include forestry, swimming, reading, and caring for his dogs and horses. He lives on a quiet lake with his wife, Nancy, four shelter dogs (Gaino, front in photo, deceased 30 September 2013; Pepto, back in photo; Peanut; and Merry), and three horses (Eddie, Gwen, and Festus).

John M. Martinko received his B.S. in Biology from Cleveland State University. He then worked at Case Western Reserve University, conducting research on the serology and epidemiology of *Streptococcus pyogenes.* His doctoral work at the State University of New York at Buffalo investigated antibody specificity and antibody idiotypes. As a postdoctoral fellow, he worked at Albert Einstein College of Medicine in New York on the structure of major histocompatibility complex proteins. Since 1981, he has been in the Department of Microbiology at Southern Illinois University Carbondale where he was Associate Professor and Chair, and Director of the Molecular Biology, Microbiology, and Biochemistry Graduate Program. His research interests centered on the structure–function relationships of immune system proteins, including immunoglobulins, T cell receptors, and major histocompatibility proteins. His teaching interests include an advanced course in immunology as well as immunology and inflammation instruction to medical students. For his educational efforts, he won the 2007 Southern Illinois University Outstanding Teaching Award. He has been active in a number of educational outreach programs for pre-university students and teachers. He has also been a faculty member at Bard College in its innovative Citizen Science program, an interactive laboratory, computer, and problem-based-learning science curriculum that introduces freshmen students to critical thinking through the discovery and application of scientific principles. He was the Chair of the Institutional Animal Care and Use Committee at SIUC and continues to act as a consultant in the area of animal care. He is also an avid golfer and cyclist. John lives in Carbondale with his wife Judy, a high school science teacher.

Kelly S. Bender received her B.S. in Biology from Southeast Missouri State University (1999) and her Ph.D. (2003) in Molecular Biology, Microbiology, and Biochemistry from Southern Illinois University Carbondale. Her dissertation work focused on the genetics of perchlorate-reducing bacteria. During her postdoctoral fellowship, Kelly worked on the genetic regulation of sulfate-reducing bacteria in the laboratory of Judy Wall at the University of Missouri–Columbia. She also completed a transatlantic biotechnology fellowship at Uppsala University in Sweden researching regulatory small RNAs in bacteria. In 2006, Kelly returned to her alma mater, Southern Illinois University Carbondale, as an Assistant Professor in the Department of Microbiology and was tenured and promoted to Associate Professor in 2012. Her lab studies a range of topics including the regulation of stress responses by small RNAs, microbial community dynamics of sites impacted by acid mine drainage, and the bioremediation of uranium by metal- and sulfate-reducing bacteria. Kelly teaches courses in microbial genetics and molecular biology, has served on numerous federal grant review panels, and is an active member of the American Society for Microbiology. Her other interests include biking, cooking, and spending time with family, friends, and her miniature schnauzer, Pepper.

Daniel H. Buckley is an Associate Professor at Cornell University in the Department of Crop and Soil Sciences. He earned his B.S. in Microbiology (1994) at the University of Rochester and his Ph.D. in Microbiology (2000) at Michigan State University. His graduate research focused on the ecology of soil microbial communities and was conducted in the laboratory of Thomas M. Schmidt in affiliation with the MSU Center for Microbial Ecology. Dan's postdoctoral research examined linkages between microbial diversity and biogeochemistry in marine microbial mats and stromatolites and was conducted in the laboratory of Pieter T. Visscher at the University of Connecticut. Dan joined the Cornell faculty in 2003. His research program investigates the ecology and evolution of microbial communities in soils with a focus on the causes and consequences of microbial diversity. He has taught both introductory and advanced courses in microbiology, microbial diversity, and microbial genomics. He received a National Science Foundation Faculty Early Career Development (CAREER) award in 2005 for excellence in integrating research and education. He has served as Director of the Graduate Field of Soil and Crop Sciences at Cornell and Codirector of the Marine Biological Laboratory Microbial Diversity Summer Course in Woods Hole, Massachusetts. He currently serves on the editorial boards of *Applied and Environmental Microbiology* and *Environmental Microbiology*. Dan lives in Ithaca, New York, with his wife Merry and sons Finn and Colin. Dan enjoys running and a variety of outdoor sports but, most of all, catching critters down at the creek with his boys.



David A. Stahl received his B.S. degree in Microbiology from the University of Washington, Seattle, and completed graduate studies in microbial phylogeny and evolution with Carl Woese in the Department of Microbiology at the University of Illinois at Urbana-Champaign. Subsequent work as a postdoctoral fellow and research associate with Norman Pace, then at the National Jewish Hospital in Colorado, involved early applications of 16S rRNA-based sequence analysis to the study of natural microbial communities. In 1984 Dave joined the faculty at the University of Illinois with appointments in Veterinary Medicine, Microbiology, and Civil Engineering. In 1994 he moved to the Department of Civil Engineering at Northwestern University, and in 2000 returned to the University of Washington as professor in the Departments of Civil and Environmental Engineering and Microbiology. Dave is known for his work in microbial evolution, ecology, and systematics, and received the 1999 Bergey Award and the 2006 ASM Procter & Gamble Award in Applied and Environmental Microbiology. He is a fellow in the American Academy of Microbiology and a member of the National Academy of Engineering. His main research interests surround the biogeochemistry of nitrogen and sulfur and the microbial communities that sustain the associated nutrient cycles. His laboratory was first to culture ammonia-oxidizing *Archaea,* a group believed to be the key mediators of this process in the nitrogen cycle. Dave has taught several courses in environmental microbiology, was one of the founding editors of the journal *Environmental Microbiology,* and has served on many advisory committees. Outside the lab, Dave enjoys hiking, bicycling, spending time with family, reading a good science fiction book, and—with his wife Lin—renovating an old farmhouse on Bainbridge Island.

Dedications

Michael T. Madigan
dedicates this book to the memory of his old friend, Snuffy. I sure miss those long walks, just you and me.

John M. Martinko
dedicates this book to his mother Lottie, who inspired all her children to achieve and excel.

Kelly S. Bender
dedicates this book to the memory of her grandmother, Alberta, whose biggest regret in life was not being able to attend school past the fifth grade.

Daniel H. Buckley
dedicates this book to Merry. Thanks for sharing this adventure and all the others.

David A. Stahl
dedicates this book to his wife, Lin. My love, and one that helps me keep the important things in perspective.

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Preface

Because learning evolves, so do we. Streamlined, completely up to date, and written with deference to the history of microbiology and excitement for the future, the Fourteenth Edition of *Brock Biology of Microorganisms* is the strongest yet. For three generations, students and instructors have relied on the accuracy, authority, consistency, and up-to-date science of *Brock Biology of Microorganisms* to learn the core principles of microbiology and pique their interest in the future of the discipline. With the Fourteenth Edition, students will benefit from the book's emphasis on cutting-edge research, its seamless integration of and introduction to modern molecular microbiology, and a visually stunning art program revision. Additionally, for the first time, *Brock Biology of Microorganisms* is supported by MasteringMicrobiology, Pearson's online homework, tutorial, and assessment system.

Experienced authors Madigan, Martinko, and Stahl welcome two new coauthors on the Fourteenth Edition: Kelly S. Bender and Daniel H. Buckley. Significantly revising the coverage of molecular biology and microbial genetics, Kelly has been highly praised for both her undergraduate teaching and graduate student mentoring at Southern Illinois University. At Cornell, Dan participates in the Cornell Institute for Biology Teachers' summer workshop for high school science teachers and codirects the world-famous Summer Course in Microbial Diversity at Woods Hole. Both new coauthors have greatly strengthened the core mission of *Brock Biology of Microorganisms*: to remain the best learning resource for today's microbiology students and instructors.

What's New in the 14th Edition?

Reorganized and reimagined, the Fourteenth Edition guides students through the six major themes of microbiology in the 21st century as outlined by the American Society of Microbiology Conference on Undergraduate Education (ASMCUE): Evolution, Cell Structure and Function, Metabolic Pathways, Information Flow and Genetics, Microbial Systems, and the Impact of Microorganisms. With enhanced and revised artwork and nearly 200 new color photos, *Brock Biology of Microorganisms* beautifully presents microbiology as the visual science it is. The new chapter-opening features, titled "MicrobiologyNow," engage students in cutting-edge research relevant to each chapter's content and connect to assignable and assessable MasteringMicrobiology coaching activities. "Explore the Microbial World" features focus on specific topics that help students get a feel for the "big picture" in microbiology while simultaneously fueling their scientific curiosity.

Genomics, and all of the various "omics" it has spawned, support content in every chapter of *Brock Biology of Microorganisms*, reflecting how the omics revolution has transformed all of biology. Gone is the day of microbiology as a descriptive science. Mastering the principles of the dynamic field of microbiology today requires understanding the underlying molecular biology. As authors, we are well aware of this, and have written *Brock Biology of Microorganisms* in a way that provides both the foundation for the science and the science itself. The result is a truly robust and eminently modern treatment of microbiology.

To strengthen the learning experience, additional MasteringMicrobiology content includes chapter-specific reading quizzes, MicroLab Tutorials, MicrobiologyNow coaching activities, Clinical Case and MicroCareer coaching activities, animation quizzes, MCAT Prep questions, and many additional study and assessment tools. Collectively, the content and presentation of *Brock Biology of Microorganisms*, coupled with the powerful learning tools of MasteringMicrobiology, create an unparalleled educational experience in microbiology.

Revision Highlights

Chapter 1

- Chapter 1 has been revised to provide an up-to-date and succinct introduction to and overview of microbiology, including basic elements of cell structure and the phylogenetic tree of life.
- The power of genomics for solving mysteries in microbiology is revealed in a new Explore the Microbial World feature, "The Black Death Decoded" on forensic studies of victims of Europe's "Black Death" outbreak over 650 years ago.

Chapter 2

- Coverage of microbial cell structure and function now combines material on *Bacteria* and *Archaea* with that of microbial eukaryotes, giving students a thorough introduction to comparative cell structure and providing the instructor with all of the tools necessary for effective classroom presentations.

Chapter 3

- The essential features of microbial metabolism necessary for understanding how microorganisms transform energy are laid out in a logical sequence with an appropriate level of detail on metabolic diversity for introductory students. Newly rendered art makes mastering key metabolisms a more visual and engaging experience.

Chapter 4

- The basic principles of molecular microbiology are heavily revised and beautifully presented early in the text to provide a useful background for students as they proceed through the book.
- Beautiful new art stresses consistency and simplicity to make complex molecular concepts easy to learn, retain, and apply.

Chapter 5

- To close Unit 1, this chapter draws on the previous four chapters in describing the end result of molecular biology and physiology: cell division and population growth.
- The chapter now incorporates the essentials of microbial growth control to allow instructors to better tie important practical content to the basic science of the growth process itself.

Chapter 6

- Complete coverage of microbial genomics and the omics revolution that is driving the science of microbiology today appears much earlier in the book than in the previous edition. Coverage of the technology, biology, and evolution of genomes is laid out in a new and exciting fashion.
- Marvel at the power of genomics in a new Explore the Microbial World feature on single-cell genomics: "Genomics, One Cell at a Time."

Chapter 7

- Chapter 7 contains major updates on the regulation of gene expression—one of the hottest areas in microbiology today—including expanded coverage of cell sensing capacities and signal transduction.
- Explore new aspects of gene regulation, including the importance of small RNAs and the regulation of special events in model bacteria such as sporulation in *Bacillus*, cell differentiation in *Caulobacter*, and heterocyst formation in the nitrogen-fixing cyanobacterium *Anabaena*.

Chapter 8

- The basic principles of virology are presented without extraneous detail and use bacteriophage T4 as a model for depicting key virological concepts.
- New coverage of the virosphere and viral ecology reveals the overwhelming genetic diversity of viruses.

Chapter 9

- Coverage of viral genomes and diversity now directly follows the basic virology chapter to better link the two closely related topics.
- New coverage of the evolution of viral genomes and a new organization that more directly contrasts the biology of DNA and RNA viruses support a more consistent and conceptual understanding of viral diversity.

Chapter 10

- Coverage of the fundamental principles of the genetics of *Bacteria* and *Archaea* is now strategically located in the book to better incorporate supporting concepts from molecular microbiology, growth, regulation, and virology.

Chapter 11

- Complete coverage of the molecular biology of gene cloning and other major genetic manipulations forms a prelude to coverage of the application of these methods in the fast-moving field of biotechnology.
- Enter the world of synthetic biology and learn how this hot new area promises yet another revolution in biology.

Chapter 12

- Microbial evolution and systematics benefits from a major revision that focuses on the mechanisms of microbial evolution, including the importance of genomic evolution and horizontal gene transfer.
- Consider how metabolic interdependencies in microbial communities may have evolved in a fascinating new Explore the Microbial World feature, "The Black Queen Hypothesis."

Chapter 13

- Microbial metabolic diversity is now presented in a single chapter to better compare and contrast the key metabolisms of *Bacteria* and *Archaea* and to emphasize how "the unity of biochemistry" has pervaded microbial metabolism.
- Metabolic diversity is now strategically positioned to naturally segue into the new chapter on bacterial functional diversity.

Chapters 14 and 15

- Chapter 14, "Functional Diversity of *Bacteria*," now explores bacterial diversity with respect to the ecological, physiological, and morphological characteristics of well-known bacteria. Chapter 15, "Diversity of *Bacteria*," presents the diversity of bacterial life in a truly phylogenetic context. New, colorful, and easy-to-follow phylogenetic trees summarize bacterial diversity in both chapters.

Chapter 16

- Archaeal diversity is revised with a stronger phylogenetic thread and new coverage of the more recently discovered archaeal phyla of *Thaumarchaeota*, *Nanoarchaeota*, and *Korarchaeota.*
- Learn how the previously unrecognized *Thaumarchaeota* are probably the most common *Archaea* on Earth and review the physicochemical limits to life, all of which are currently defined by species of *Archaea*.

Chapter 17

- Eukaryotic microbial diversity benefits from new phylogenetic coverage and a chapter prelude on the importance of endosymbioses in the evolution of eukaryotic cells.
- Many new color micrographs portray the beauty and diversity of eukaryotic microbial life.

Chapter 18

- The modern tools of the microbial ecologist are described with examples of how each has sculpted the science. Also, learn how the omics revolution has provided a new window for simplifying complex problems in microbial ecology.
- In the new Explore the Microbial World feature "Culturing the Uncultured," discover how novel ecological methods have yielded laboratory cultures of the marine bacterium *Pelagibacter*, the most abundant organism on Earth.

Chapter 19

- The properties and microbial diversity of the major microbial ecosystems are compared and contrasted in an exciting new way.
- New environmental census data for freshwater habitats and the microbial ecology of arid landscapes highlight new material in this chapter, along with fresh coverage of the link between marine microorganisms and climate change.

Chapter 20

- Chapter 20 includes new coverage of the remarkable abilities of microorganisms to respire solid metal oxides in the iron and manganese cycles.
- Learn how humans are profoundly affecting the nitrogen and carbon cycles, including inorganic nutrient overloads and other forms of pollution, and how all of this feeds back into climate change.

Chapter 21

- A new chapter on the "built environment" shows how humans create new microbial habitats through construction of buildings, supporting infrastructure, and habitat modification. Witness the substantial positive and negative effects microorganisms have on important human infrastructure including wastewater treatment, microbial mining and acid mine drainage, corrosion of metals, the biodeterioration of stone and concrete, and the problem of pathogens in drinking water.

Chapter 22

- Here you will find expanded coverage of how microorganisms profoundly affect the physiology of plants and animals through symbiotic associations, including the dynamic topic of the human microbiome and its relationship to health and disease.
- Discover how a common mechanism used by bacteria and fungi to form symbiotic associations with the roots of plants provides the plants with key nutrients.

Chapter 23

- Major topics in human microbiology including the normal microflora, pathogenesis, and host factors in infection and disease are presented in a style that unites these concepts and reveals how they tip the balance toward health or disease.

Chapter 24

- Chapter 24 is designed to be the straightforward and concise overview of immunology that many instructors use to teach the fundamental concepts of the science.
- This chapter is loaded with practical information on vaccines, inflammation, and allergic responses in an easily teachable format.

Chapter 25

- Built on the shoulders of the previous chapter, Chapter 25 offers a more complete picture of immune mechanisms, with an emphasis on the molecular and cellular interactions that control innate and adaptive immunity.

Chapter 26

- This is a brief chapter that considers immunology from a completely molecular perspective, including the important receptor–ligand interactions that trigger the immune response and the genetics of the key proteins that drive adaptive immunity.

Chapter 27

- Reorganized and up to date, Chapter 27 describes the role of the clinical microbiologist and introduces the tools used to identify and track infectious diseases in clinical laboratories.
- New coverage of antimicrobial agents and their clinical usage underscores the important role of both drug therapy and drug resistance in medicine today.

Chapter 28

- A revised discussion of epidemiology introduces the concept of the reproduction number (R) and its implications for disease spread and control by herd immunity.
- Find up-to-date coverage of emerging infectious diseases and current pandemics, including those of HIV/AIDS, cholera, and influenza, and the role of the epidemiologist in public health microbiology.

Chapter 29

- Coverage of diseases transmitted from person to person is reorganized and illustrated with dozens of new color photos showing symptoms and treatments. To better consolidate material that fits a common theme, infectious diseases in this and each of the next three chapters are presented by taxonomy.

Chapter 30

- Bacterial and viral diseases transmitted by insect vectors or from soil are consolidated and illustrated by dozens of new color photos.
- This chapter contains new coverage of important viral diseases such as yellow fever and dengue fever and the bacterial diseases anthrax, tetanus, and gas gangrene.

Chapter 31

- Common-source diseases linked to contaminated food and water are now consolidated to better emphasize their similar modes of transmission. Coverage within the chapter is by taxonomy—bacterial versus viral—and illustrated with nearly 30 new color photos.
- Find new coverage of the potentially fatal foodborne infection caused by the intracellular bacterium *Listeria*.

Chapter 32

- All infectious diseases caused by eukaryotic microorganisms—fungi and parasites—are consolidated into one chapter to retain the taxonomic theme of medical microbiology. The visual experience is bolstered by 35 new color photos showing the pathogens and disease symptoms. Coverage of fungal and microbial parasitic diseases is expanded; the chapter also includes first-time coverage of major helminthic infections.

Other Learning Tools

- Two appendices, including a primer on bioenergetic calculations and a list of higher order taxa described in *Bergey's Manual of Systematic Bacteriology*; a glossary; and a thorough index round out the learning package in *Brock Biology of Microorganisms*, 14e.

Acknowledgments

A textbook is a complex entity and emerges from the contributions of a large book team. Besides the authors, the team is composed of folks both inside and outside of Pearson. Acquisitions Editor Kelsey Churchman and Associate Editor Nicole McFadden, both of Pearson, were the workhorses in editorial. Kelsey paved the way for the Fourteenth Edition of *Brock Biology of Microorganisms* (*BBOM* 14e) and skillfully maneuvered the book around the challenges inherent in any major textbook project. Nicole ran the day-to-day operations of the *BBOM* team, expertly processing the manuscript and keeping all facets of the project on track. The authors thank Kelsey and Nicole for their dedication to *BBOM* and professionalism in seeing the Fourteenth Edition through to completion.

The *BBOM* 14e production and design team in San Francisco was composed of Michele Mangelli (Mangelli Productions), Yvo Riezebos (Tandem Creative, Inc.), and Elisheva Marcus (Pearson). Michele managed the production team and kept everyone on mission and on budget. The artistic magic of Yvo is clearly visible in the beautiful text and cover designs of *BBOM* 14e. Elisheva (Ellie) was our art development editor and created the new art look for *BBOM* 14e, one that readers will immediately appreciate for its clarity, consistency, and modern style. Ellie's strong background in both science and art will be obvious throughout the book and her contributions were a major improvement to this edition. Thank you, Michele, Yvo, and Ellie. The authors also thank the art team at Imagineering (Toronto) for helping the authors convey a strong educational message and for their excellent suggestions for art improvements.

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Robert Blankenship, *Washington University St. Louis*
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CHAPTER

1 · Microorganisms and Microbiology

microbiology**now**

Microbial Life Is Everywhere

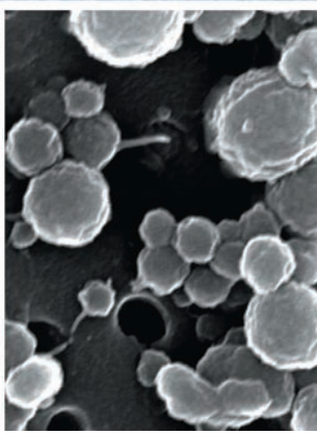
As you embark on your journey to the microbial world, you will be astounded to learn where microorganisms live in nature. In brief, they live everywhere, including locations too harsh for macroorganisms. For example, a research team studying the permanently ice-covered Lake Vida in the McMurdo Dry Valleys of Antarctica (top photo) found living bacteria immersed in a subfreezing salt solution at −13°C! These hardy microorganisms were discovered by microbiologists wearing protective clothing to prevent contamination during the drilling process (bottom photos).

The Lake Vida bacteria, a metabolic group called psychrophiles (a term that means "cold loving"), were shown to carry out various metabolic reactions at the temperature of their icy home. Specific genes isolated from the various Lake Vida bacteria were used to classify the organisms, and future studies of their genetic blueprints—their genomes—should help to reveal the genetic secrets that allow these organisms to thrive in the constant cold.

Lake Vida is unusual even for Antarctic lakes, since its ice cover extends all the way to the bottom. Sunlight, only available 6 months of the year, cannot penetrate deeply into the lake. So the Lake Vida bacteria are probably metabolizing and growing, albeit extremely slowly, on organic carbon that was trapped in the ice at the time the lake became ice-sealed, millennia ago.

Microbiologists study bacteria from extreme environments to reveal the environmental limits to life and to search for unique products that might benefit humans or our planet. But in addition to contributing to basic and applied science, the Lake Vida bacteria are models for the kinds of life forms that could inhabit other icy worlds, such as Mars, or Jupiter's moon, Europa.

Murray, A.E., et al. 2012. Microbial life at −13°C in the brine of an ice-sealed Antarctic lake. *Proc. Natl. Acad. Sci.* (*USA*). *109:* 20626–20631.



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I • Introduction and Major Themes of Microbiology

1.1 What Is Microbiology About and Why Is It Important?

The science of microbiology is all about **microorganisms** and how they work, especially the bacteria, a very large group of very small cells (Figure 1.1) that have enormous basic and practical importance. Microbiology is also about diversity and evolution of microbial cells, about how different kinds of microorganisms arose and why. Microbiology embraces ecology, so it is also about where microorganisms live on Earth, how they associate and cooperate with each other, and what they do in the world at large, in soils and waters and in animals and plants.

The science of microbiology revolves around two interconnected themes: (1) understanding the nature and functioning of the microbial world, and (2) applying our understanding of the microbial world for the benefit of humankind and planet Earth. As a *basic* biological science, microbiology uses microbial cells to probe the fundamental processes of life. In so doing, microbiologists have developed a sophisticated understanding of the chemical and physical basis of life and have learned that all cells share much in common. As an *applied* biological science, microbiology is at the forefront of many important breakthroughs in human and veterinary medicine, agriculture, and industry. From infectious diseases to soil fertility to the fuel you put in your automobile, microorganisms affect the everyday lives of humans in both beneficial and detrimental ways.

Microorganisms existed on Earth for billions of years before plants and animals appeared, and we will see later that the genetic and physiological diversity of microbial life dwarfs that of the plants and animals. Although microorganisms are the smallest forms of life (Figure 1.1), collectively they constitute the bulk of biomass on Earth and carry out many necessary chemical reactions for higher organisms. In the absence of microorganisms, higher life forms would never have appeared and could not be sustained. Indeed, the very oxygen we breathe is the result of past microbial activity. Moreover, humans, plants, and animals are intimately dependent on microbial activities for the recycling of key nutrients and for degrading organic matter. It is thus safe to say that no other life forms are as important as microorganisms for the support and maintenance of life on Earth.

This chapter begins our journey into the microbial world. Here we will begin to discover what microorganisms are and what they do and explore their evolutionary history and impact on planet Earth. We will also place microbiology in historical context, as a process of scientific discovery. From the landmark contributions of both early microbiologists and scientists practicing today, the microbial world will begin to unfold.

MINIQUIZ

- If microbial life had not evolved, would you be here today? Give one good reason why or why not.
- Why are microbial cells useful tools for basic science? Why are microorganisms important to humans?

1.2 Structure and Activities of Microbial Cells

Microbial cells are living compartments that interact with their environment and with other cells in dynamic ways. In Chapter 2 we will examine the structure of cells in detail and relate specific structures to specific functions. Here we present a snapshot of

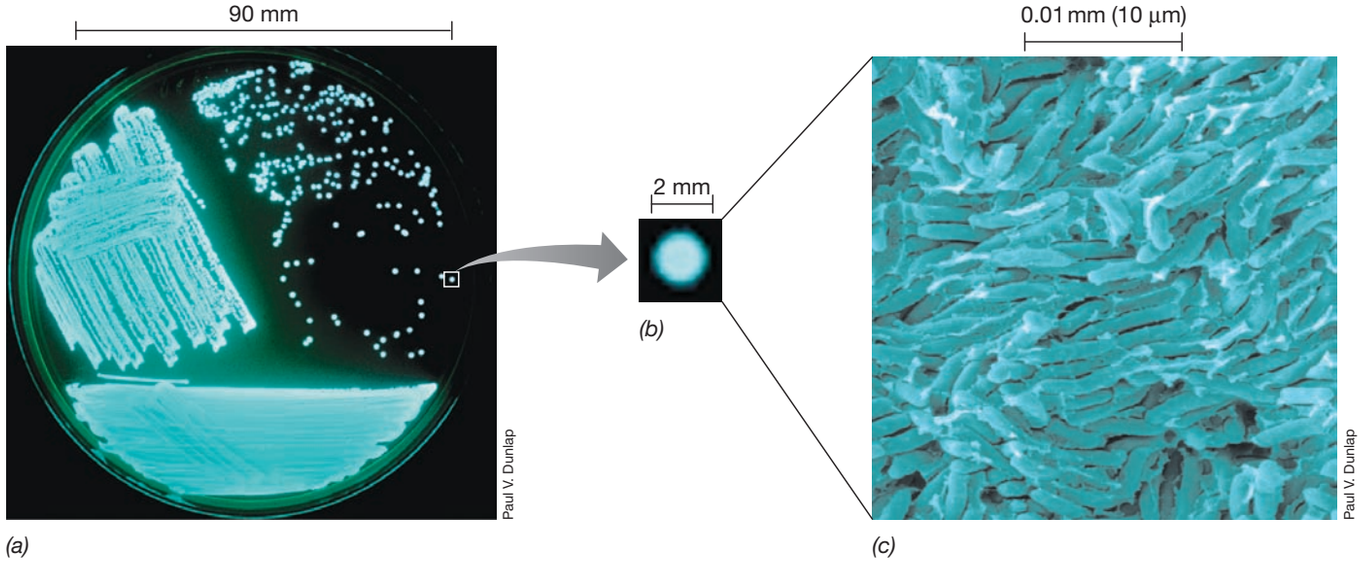


Figure 1.1 **Microbial cells.** *(a)* Bioluminescent (light-emitting) colonies of the bacterium *Photobacterium* grown in laboratory culture on a Petri plate. *(b)* A single colony can contain more than 10 million (10^7) individual cells. *(c)* Scanning electron micrograph of cells of *Photobacterium.*

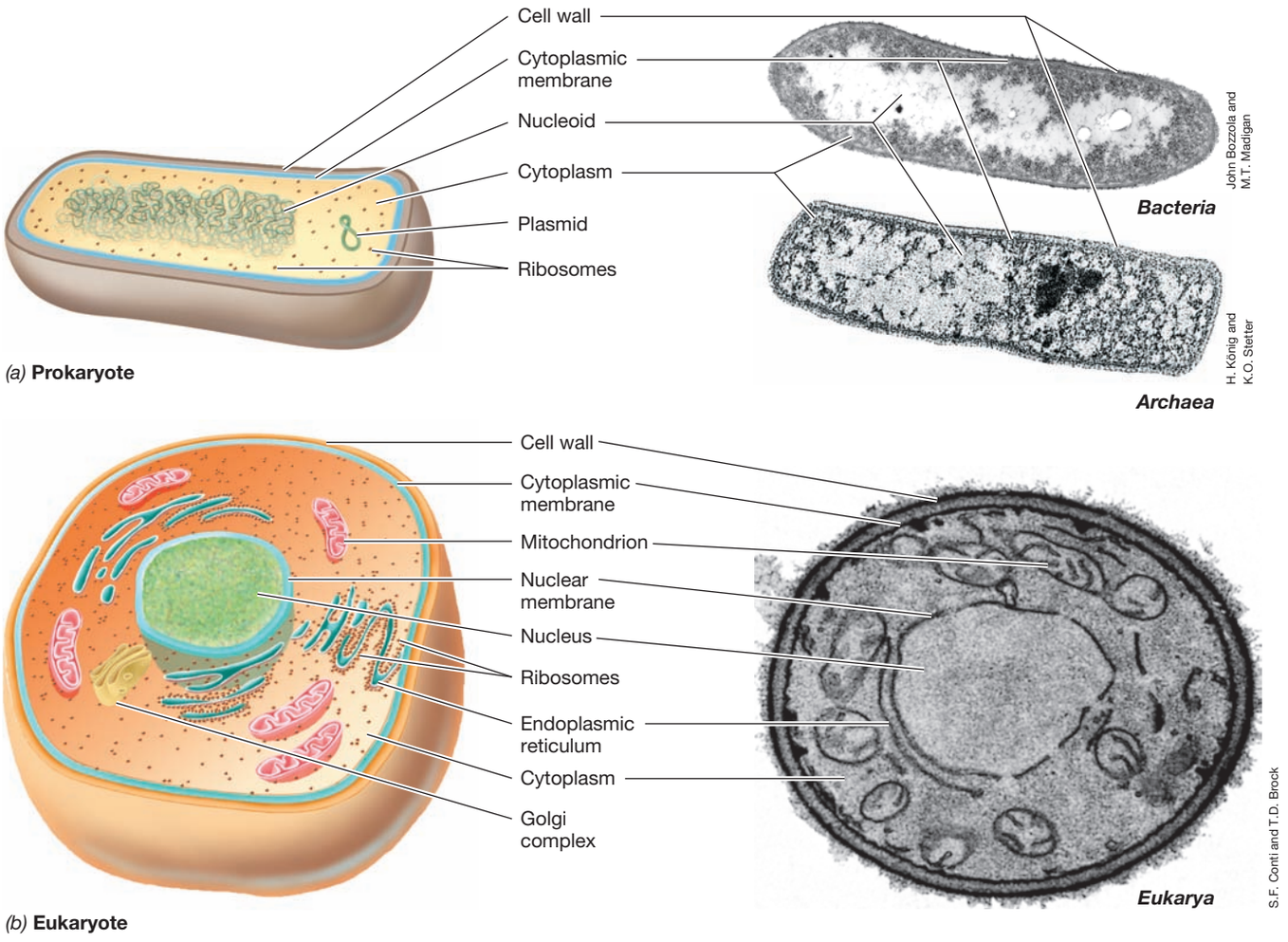


Figure 1.2 **Microbial cell structure.** *(a)* (Left) Diagram of a prokaryotic cell. (Right) Electron micrograph of *Heliobacterium modesticaldum* (*Bacteria,* cell is about 1 μm in diameter) and *Thermoproteus neutrophilus* (*Archaea,* cell is about 0.5 μm in diameter). *(b)* (Left) Diagram of a eukaryotic cell. (Right) Electron micrograph of a cell of *Saccharomyces cerevisiae* (*Eukarya,* cell is about 8 μm in diameter).

microbial structure and activities. We purposely exclude viruses in this discussion because although they resemble cells in many ways, viruses are not cells but instead a special category of microorganism. We consider the structure, diversity, and activities of viruses in Chapters 8 and 9.

Elements of Microbial Structure

All cells have much in common and contain many of the same components (Figure 1.2). All cells have a permeability barrier called the **cytoplasmic membrane** that separates the inside of the cell, the **cytoplasm**, from the outside. The cytoplasm is an aqueous mixture of **macromolecules**—proteins, lipids, nucleic acids, and polysaccharides—small organic molecules (mainly precursors of macromolecules), various inorganic ions, and **ribosomes**, the cell's protein-synthesizing structures. The **cell wall** lends structural strength to a cell; it is a relatively permeable structure located outside the membrane and is a much stronger layer than the membrane itself. Plant cells and most microorganisms have cell walls, whereas animal cells, with rare exceptions, do not.

Examination of the internal structure of cells reveals two patterns, called **prokaryote** and **eukaryote**. Prokaryotes include the *Bacteria* and the *Archaea* and consist of small and structurally rather simple cells (Figure 1.2*a*). Eukaryotes are typically much larger than prokaryotes and contain an assortment of membrane-enclosed cytoplasmic structures called **organelles** (Figure 1.2*b*). These include, most prominently, the DNA-containing nucleus but also mitochondria and chloroplasts, organelles that specialize in supplying the cell with energy, and various other organelles. Eukaryotic microorganisms include algae, protozoa and other protists, and the fungi. The cells of plants and animals are also eukaryotic. Despite the clear-cut *structural* differences between prokaryotes and eukaryotes (Figure 1.2), the word "prokaryote" does not imply *evolutionary* relatedness. As we will see in the next section, although species of *Bacteria* and *Archaea* may *look* similar, they are not closely related in an evolutionary sense.

Genes, Genomes, Nucleus, and Nucleoid

The life processes of a cell are controlled by its complement of genes, its **genome**. A gene is a segment of DNA that encodes a

protein or an RNA molecule. The genome is the living blueprint of an organism; the characteristics, activities, and very survival of a cell are governed by its genome. The genomes of prokaryotes and eukaryotes are organized differently. In eukaryotes, DNA is present as linear molecules within the membrane-enclosed **nucleus**. By contrast, the genome of *Bacteria* and *Archaea* is a closed circular chromosome (a few prokaryotes have linear chromosomes). The chromosome aggregates within the cell to form the **nucleoid**, a mass visible in the electron microscope (Figure 1.2*a*). Most prokaryotes have only a single chromosome, but many also contain one or more small circles of DNA distinct from that of the chromosome, called *plasmids*. Plasmids typically contain genes that confer a special property on the cell (such as a unique metabolism, or antibiotic resistance) rather than essential genes needed under all growth conditions. This contrasts with genes on the chromosome, most of which are needed for basic survival.

How many genes does a cell have? We know that this number is highly variable because of the many genomes that have been sequenced. The genome of the model bacterium *Escherichia coli* is fairly typical in size; it is a single circular chromosome of 4,639,221 base pairs of DNA arranged into 4288 genes. The genomes of a few prokaryotes are three times this size while the genomes of some others contain as few as one-twentieth as many genes. Eukaryotic cells typically have much larger genomes than do prokaryotes. A human cell, for example, contains over 1000 times as much DNA as a cell of *E. coli* and about 7 times as many genes.

Activities of Microbial Cells

What activities do microbial cells carry out? We will see that in nature, microbial cells typically live in groups called *microbial communities*. Figure 1.3 considers some of the ongoing cellular activities within the microbial community. All cells show some form of **metabolism** by taking up nutrients from the environment and transforming them into new cell materials and waste products. During these transformations, energy is conserved that can be used by the cell to support synthesis of new structures. Production of these new structures culminates in the division of the cell to form two cells. In microbiology, we use the word **growth** to refer to the increase in cell number as a result of cell division.

During metabolism and growth, both genetic and catalytic events occur in cells; biological information flow is initiated and metabolic pathways are engaged. On the genetic side, the cell's genome is replicated, and the proteins needed to support growth under a given set of conditions are biosynthesized in the sequential processes of *transcription* and *translation* (Figure 1.3). These events require that the cell's catalytic machinery—its **enzymes**—carry out reactions that supply the energy and precursors necessary for the biosynthesis of all cell components. Catalytic and genetic events in a microbial cell are coordinated and highly regulated to ensure that new cell materials are made in the proper order and concentrations and that the cell remains optimally tuned to its surroundings.

Many microbial cells are capable of **motility**, typically by self-propulsion (Figure 1.3). Motility allows cells to move away from unfavorable conditions and to exploit new resources or growth opportunities. Some microbial cells undergo **differentiation**, which

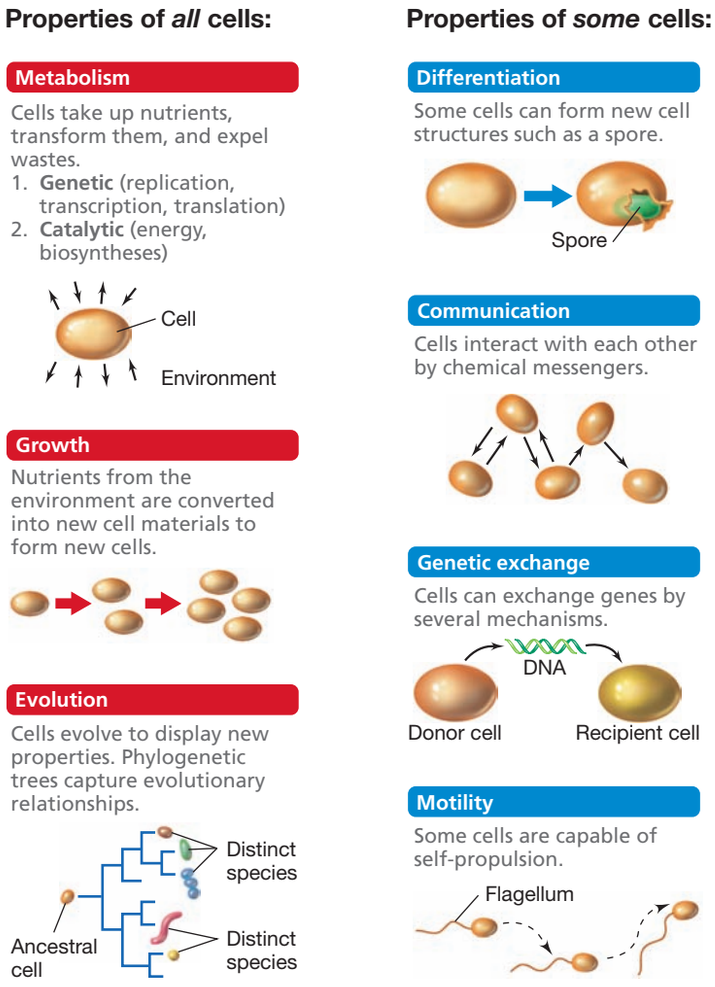


Figure 1.3 The properties of microbial cells. Major activities ongoing in cells in the microbial community are depicted.

may result in the formation of modified cells specialized for growth, dispersal, or survival. Cells respond to chemical signals in their environment, including those produced by other cells of either the same or different species, and these signals often trigger new cellular activities. Microbial cells thus exhibit intercellular **communication**; they are "aware" of their neighbors and can respond accordingly. Many prokaryotic cells can also transfer genes to or accept genes from neighboring cells, either of the same species or of a different species, in the process of **genetic exchange**.

Evolution (Figure 1.3) is the process of descent with modification in which genetic variants (mutants) are selected based on their reproductive fitness. Although we learn from elementary biology that evolution is a very slow process, evolution in microbial cells can be very rapid when selective pressure is strong. For example, witness today how genes encoding antibiotic resistance in pathogenic (disease-causing) bacteria have been selected and widely distributed by the indiscriminate use of antibiotics in human and veterinary medicine. Genetic exchange between prokaryotic cells, which is independent of evolution (Figure 1.3), can also significantly accelerate the adaptation of cells to new habitats or to rapidly changing conditions.

Not all of the processes depicted in Figure 1.3 occur in all cells. Metabolism, growth, and evolution, however, are universal. We now take a peek at the results of microbial evolution in the form of the enormous diversity of the microbial world that has been unveiled by modern microbiology.

MINIQUIZ

- What important functions do the following play in a cell: cytoplasmic membrane, ribosomes, cell wall?
- What type of cells have a nucleus? Nucleoid? What is a cell's genome and why is it important?
- What do the terms "growth" and "motility" mean in microbiology?

1.3 Evolution and Diversity of Microbial Cells

Microorganisms were the first entities on Earth that showed the properties we associate with life. How did microbial cells originate and how are extant microbial cells related to one other?

The First Cells and the Beginnings of Evolution

Because all cells are constructed in similar ways, it is thought that all cells have descended from a common ancestral cell, the *last universal common ancestor* (LUCA). After the first cells arose from nonliving materials, a process that occurred over hundreds of millions of years, their subsequent growth formed cell populations and these began to interact with other cell populations to form microbial communities. Along the way, evolution and genetic exchange served up variants that could be selected for improvements that made their success and survival more probable. Today we see the grand result of these processes, ongoing for nearly 4 billion years.

Life on Earth through the Ages

Earth is 4.6 billion years old and evidence shows that microbial cells first appeared between 3.8 and 3.9 billion years ago (Figure 1.4). During the first 2 billion years of Earth's existence, its atmosphere was anoxic (O_2 was absent), and only nitrogen (N_2), carbon dioxide (CO_2), and a few other gases were present. Only microorganisms capable of anaerobic metabolisms could survive under these conditions. The evolution of phototrophic microorganisms—organisms that harvest energy from sunlight—occurred within 1 billion years of the formation of Earth. The first phototrophs were relatively simple ones, such as purple or green bacteria and other anoxygenic (non-oxygen-evolving) phototrophs (Figure 1.5*a*). Cyanobacteria (oxygen-evolving phototrophs) (Figure 1.5*b*) evolved from anoxygenic phototrophs nearly a billion years later and began the slow process of oxygenating Earth's atmosphere. Triggered by increases in O_2 in the atmosphere, multicellular life forms eventually evolved and continued to increase in complexity, culminating in the plants and animals we know today. But plants and animals have only existed for about half a billion years. The timeline of life on Earth (Figure 1.4*a*) shows that 80% of life's history was exclusively microbial, and thus in many ways, Earth can be considered a microbial planet.

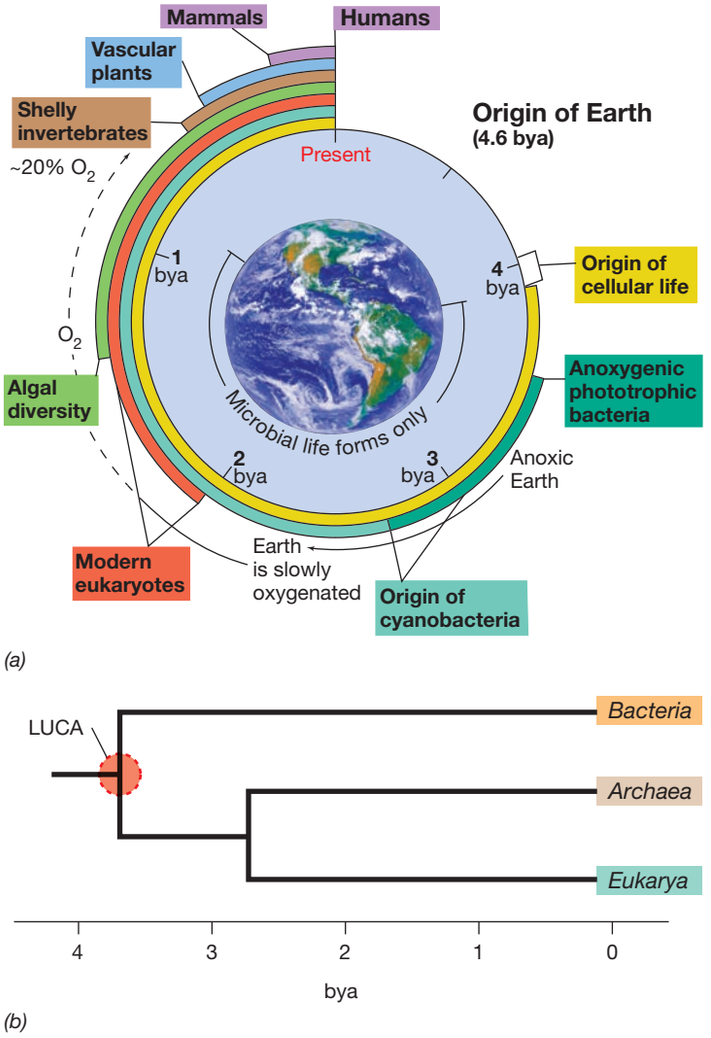


Figure 1.4 A summary of life on Earth through time and origin of the cellular domains. *(a)* Cellular life was present on Earth by 3.8 billion years ago (bya). Cyanobacteria began the slow oxygenation of Earth about 3 bya, but current levels of O_2 in the atmosphere were not achieved until 500–800 million years ago. Eukaryotes are nucleated cells (Figure 1.2*b*) and include both microbial and multicellular organisms. *(b)* The three domains of cellular organisms are *Bacteria, Archaea,* and *Eukarya. Archaea* and *Eukarya* diverged long before nucleated cells with organelles ("modern eukaryotes" in part a) appear in the fossil record. LUCA, last universal common ancestor.

As evolutionary events unfolded, three major lineages of microbial cells—the *Bacteria*, the *Archaea*, and the *Eukarya* (Figure 1.4*b*)—were distinguished; microbial *Eukarya* were the ancestors of the plants and animals. These major cell lineages are called **domains**. Over enormous periods of time, natural selection filled every suitable environment on Earth with microorganisms whose ancestry can be traced back to one of these three domains.

Microbial Diversity

Assessing the phylogenetic history of the microbial world—and thus revealing its true diversity—had to wait until tools were available that could do the job. Unlike plants and animals for which bones, fossils, leaves, and the like can be used to help reconstruct

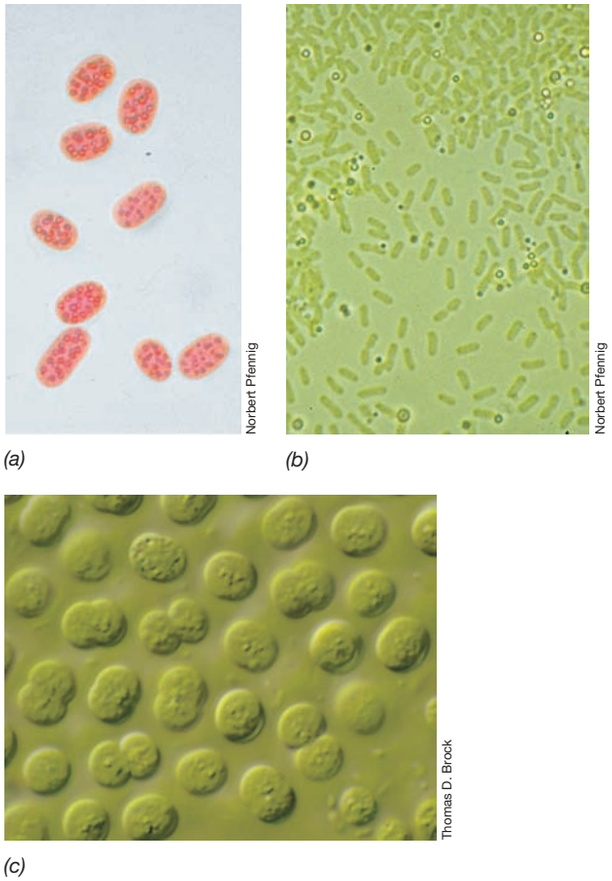


Figure 1.5 **Phototrophic microorganisms.** *(a)* Purple sulfur and *(b)* green sulfur bacteria (both anoxygenic phototrophs). *(c)* Cyanobacteria (oxygenic phototrophs). Purple and green bacteria appeared on Earth long before oxygenic phototrophs evolved (see Figure 1.4*a*).

phylogenies, such remains were unavailable to guide the construction of a microbial evolutionary tree. However, discoveries made in the past 40 years or so have clearly shown that each cell contains a record of its evolutionary history embedded in its genes. For reasons that will be presented in later chapters, genes that encode *ribosomal RNAs* have emerged as excellent barometers of microbial diversity. Ribosomal RNAs are components of ribosomes (Figure 1.2), the structures that synthesize new proteins as part of the process of translation. The technology for revealing the phylogeny of a microorganism from its ribosomal RNA genes is well developed, and from only a few cells, a phylogenetic tree that reveals the position of any organism relative to its neighbors can be constructed (Figure 1.6*a*).

As the ribosomal RNA phylogenetic tree of life has been fleshed out (Figure 1.6*b*), it has shown that thousands of species of *Bacteria* and *Archaea* exist as well as hundreds of species of microbial *Eukarya* (the tree in Figure 1.6*b* shows only a few landmark lineages). The tree of life has also revealed two important facts that were previously unsuspected: (1) *Bacteria* and *Archaea* are phylogenetically distinct despite sharing many structural features (Figure 1.2*a*), and (2) *Archaea* are more closely related to *Eukarya* than to *Bacteria*. From the last universal common ancestor of all cells (Figure 1.4*b*), evolution proceeded along two paths to form the domains *Bacteria* and *Archaea*. At some later time, the domain *Archaea* diverged to distinguish the *Eukarya* from the *Archaea* (Figures 1.4*b* and 1.6*b*).

The tools for generating microbial phylogenies on pure cultures of microorganisms (Figure 1.6*a*) have been adapted for use in natural environments in order to probe the diversity of microbial communities. These techniques have greatly improved our picture of microbial diversity and have led to the staggering conclusion that most microorganisms that exist on Earth have yet to be brought into laboratory culture! It now appears that our understanding of microbial diversity is still in its infancy. Nevertheless, the universal tree of life provides us with a roadmap to guide future work on microbial diversity and has unveiled the previously hidden concept of three evolutionary domains of life.

MINIQUIZ

- How old is Earth and when did cells first appear on Earth?
- Why were cyanobacteria so important in the evolution of life on Earth?
- How can the phylogenetic history of microorganisms be determined?
- Name the three domains of life.

1.4 Microorganisms and Their Environments

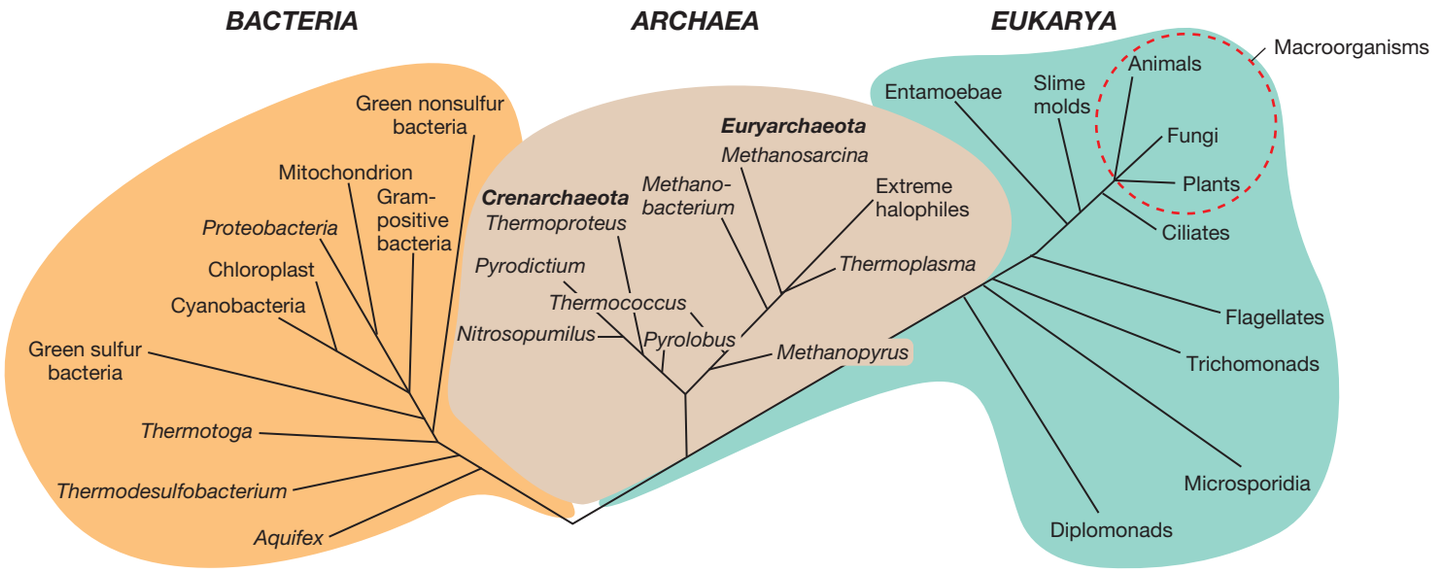
In nature, microbial cells live in association with other cells. A *population* is a group of cells derived from a single parental cell by successive cell divisions. The immediate environment in which a microbial population lives is called its **habitat**. Populations of cells interact with other populations in **microbial communities** (Figure 1.7). The abundance and diversity of any microbial community is strongly controlled by the *resources* (foods) available and *conditions* (temperature, pH, presence or absence of oxygen, and so on) that prevail in that community.

Microbial Ecosystems

Microbial populations can interact with each other in beneficial, neutral, or harmful ways. For example, the metabolic waste products of one group of organisms can be nutrients or even poisons to other groups of organisms. Habitats differ markedly in their characteristics, and a habitat that is favorable for the growth of one organism may be harmful for another. Collectively, we call all the living organisms, together with the physical and chemical components of their environment, an **ecosystem**. Major microbial ecosystems are *aquatic* (oceans, ponds, lakes, streams, ice, hot springs), *terrestrial* (surface soils, deep subsurface), and *higher organisms* (in or on plants and animals).

An ecosystem is greatly influenced by microbial activities. Microorganisms carrying out metabolic processes remove nutrients from the ecosystem and use them to build new cells. At the same time, they excrete waste products back into the

(a)



(b)

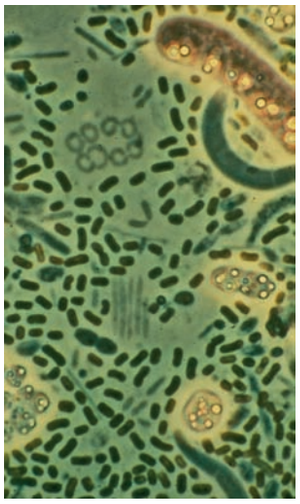
Figure 1.6 **Evolutionary relationships and the phylogenetic tree of life.** *(a)* The technology behind ribosomal RNA gene phylogenies. 1. DNA is extracted from cells. 2. Copies of the gene encoding rRNA are made by the polymerase chain reaction (PCR; ↻ Section 11.3). 3, 4. The gene is sequenced and the sequence aligned with sequences from other organisms. A computer algorithm makes pairwise comparisons at each base and generates a phylogenetic tree, 5, that depicts evolutionary relationships. In the example shown, the sequence differences are highlighted in yellow and are as follows: organism 1 versus organism 2, three differences; 1 versus 3, two differences; 2 versus 3, four differences. Thus organisms 1 and 3 are closer relatives than are 2 and 3 or 1 and 2. *(b)* The phylogenetic tree of life. The tree shows the three domains of organisms and a few representative groups in each domain.

environment. Thus, microbial ecosystems expand and contract, depending on the resources and conditions available and the different populations of organisms they can support. Over time, the metabolic activities of microorganisms can gradually change their ecosystems, both chemically and physically. For example, molecular oxygen (O_2) is a vital nutrient for some microorganisms but a poison to others. If aerobic (oxygen-consuming) microorganisms remove O_2 from a habitat, rendering it anoxic (O_2-free), the changed conditions may favor the growth of anaerobic microorganisms that were formerly present in the habitat but unable to grow. In other words, as resources and conditions change in a microbial habitat, cell populations rise and fall, changing the makeup of the community and redefining the ecosystem. In later chapters we will return to a consideration of the ways in which microorganisms affect animals, plants, and the whole global ecosystem. This is the science of **microbial ecology**, perhaps the most exciting subdiscipline of microbiology today.

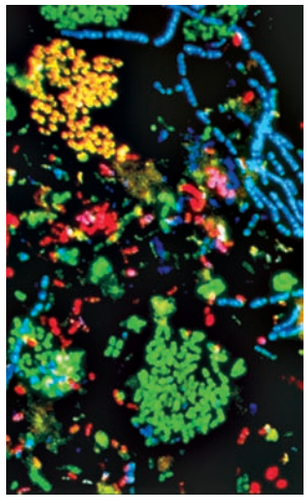
Microorganisms in Natural Environments

Microorganisms are present everywhere on Earth that will support life. These include habitats we are all familiar with—soil, water, animals, and plants—as well as virtually any structures made by humans. In the human body alone, microbial cells outnumber our body cells by a factor of ten. Sterility (the absence of life forms) in any natural sample is extremely rare.

In some microbial habitats higher organisms cannot survive because the habitat is too hot or too cold, too acidic or too caustic, too salty or otherwise osmotically stressing, or includes enormous pressures. Although one might predict that such "extreme environments" would pose challenges for any life forms, these punishing habitats are often teeming with microorganisms. Such



(a)



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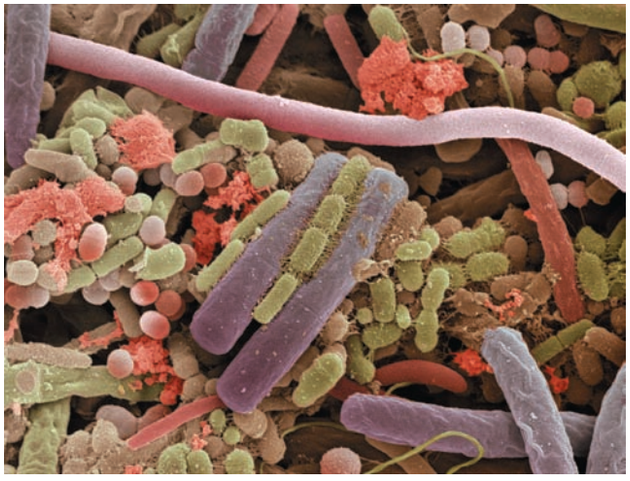

(c)

Figure 1.7 **Microbial communities.** *(a)* A bacterial community that developed in the depths of a small Michigan lake, showing cells of various green and purple (large cells with sulfur granules) phototrophic bacteria. *(b)* A bacterial community in a sewage sludge sample. The sample was stained with a series of dyes, each of which stained a specific bacterial group. From *Journal of Bacteriology 178:* 3496–3500, Fig. 2b. © 1996 American Society for Microbiology. *(c)* Scanning electron micrograph of a microbial community scraped from a human tongue.

microorganisms are called **extremophiles** and include a large and remarkable group of mainly *Bacteria* and *Archaea*, whose collective properties define the physiochemical limits to life (Table 1.1).

Extremophiles abound in such harsh environments as volcanic hot springs; on or in the ice covering lakes (see page 1), glaciers, or the polar seas; in extremely salty bodies of water; in soils and waters having a pH as low as 0 or as high as 12; and in the deep sea or deep in the earth where pressures can exceed atmospheric by over 1000 times. Interestingly, these prokaryotes do not just *tolerate* their particular environmental extreme but actually *require* it in order to grow. That is why they are called extremophiles (the suffix *-phile* means "loving"). Table 1.1 summarizes the current "record holder" extremophiles, lists the term used to describe each class, and gives examples of their habitats. We will revisit many of these organisms in later chapters and discover the special structural and biochemical properties that allow them to thrive under extreme conditions.

Estimates of the total number of microbial cells on Earth are about 2.5×10^{30} (Table 1.2). The total amount of carbon present in all of these microbial cells equals that of all plants on Earth, and plant carbon far exceeds animal carbon. Moreover, the collective contents of nitrogen and phosphorus in microbial cells exceed that of all plant biomass by 10-fold. Thus, microbial cells, small as they are, are not inconsequential; they constitute the major fraction of biomass on Earth and are key reservoirs of essential nutrients for life. We will see later that this very large number of very small cells also play important roles in many hot-button global issues such as climate change, agricultural productivity, fuels, and many other issues of importance to humans.

Most microbial cells reside in just a few very large habitats, and strange as it may seem, most do not reside on Earth's *surface* but instead lie underground in the oceanic and terrestrial subsurfaces at depths up to about 10 km (Table 1.2). By comparison to the subsurface, surface soils and waters contain a relatively small percentage of the total microbial cells on Earth. Animals (including humans), which are heavily colonized with microorganisms, collectively contain only a tiny fraction of the total microbial population of Earth (Table 1.2). Because almost everything we know about microbial life has emerged from the study of surface-dwelling microorganisms, many new discoveries are likely in store for future microbiologists who dig into Earth's most populated microbial habitats—those which we cannot see.

MINIQUIZ

- How does a microbial community differ from a microbial population?
- What is a habitat? How can microorganisms change the characteristics of their habitats?
- What is an extremophile?
- Where do most microorganisms live in nature?

1.5 The Impact of Microorganisms on Humans

Through the years microbiologists have made great strides in discovering how microorganisms work, and application of this knowledge has greatly advanced human health and welfare. Besides understanding microorganisms as agents of disease, microbiology has made great advances in understanding the important role that microorganisms play in food and agriculture, and microbiologists have been able to exploit microbial activities to produce valuable human products, generate energy, and clean up the environment.

Microorganisms as Agents of Disease

The statistics summarized in Figure 1.8 show how microbiologists and clinical medicine have combined to conquer infectious diseases

Table 1.1 Classes and examples of extremophiles[a]

Extreme	*Descriptive term*	*Genus/species*	*Domain*	*Habitat*	*Minimum*	*Optimum*	*Maximum*
Temperature							
High	Hyperthermophile	*Methanopyrus kandleri*	*Archaea*	Undersea hydrothermal vents	90°C	106°C	122°C[b]
Low	Psychrophile	*Psychromonas ingrahamii*	*Bacteria*	Sea ice	–12°C	5°C	10°C
pH							
Low	Acidophile	*Picrophilus oshimae*	*Archaea*	Acidic hot springs	–0.06	0.7[c]	4
High	Alkaliphile	*Natronobacterium gregoryi*	*Archaea*	Soda lakes	8.5	10[d]	12
Pressure	Barophile (piezophile)	*Moritella yayanosii*	*Bacteria*	Deep ocean sediments	500 atm	700 atm[e]	>1000 atm
Salt (NaCl)	Halophile	*Halobacterium salinarum*	*Archaea*	Salterns	15%	25%	32% (saturation)

[a]The organisms listed are the current "record holders" for growth in laboratory culture at the extreme condition listed.
[b]Anaerobe showing growth at 122°C only under several atmospheres of pressure.
[c]*P. oshimae* is also a thermophile, growing optimally at 60°C.
[d]*N. gregoryi* is also an extreme halophile, growing optimally at 20% NaCl.
[e]*M. yayanosii* is also a psychrophile, growing optimally near 4°C.

in the past 100 years. At the beginning of the twentieth century, the major causes of human death were infectious diseases caused by bacterial and viral **pathogens**. In those days children and the aged in particular succumbed in large numbers to microbial diseases. Today, however, infectious diseases are much less deadly, at least in developed countries. Control of infectious disease has come from a combination of advances including our increased understanding of disease processes, improved sanitary and public health practices, active vaccine campaigns, and the widespread use of antimicrobial agents, such as antibiotics. As we will see in the second part of this chapter, the development of microbiology as a science can be traced to pioneering studies of infectious disease.

Although many infectious diseases are now controlled, many others can still be a threat, particularly in developing countries. For example, diseases such as malaria, tuberculosis, cholera, African sleeping sickness, measles, pneumonia and other respiratory diseases, and diarrheal syndromes are still common in developing countries. Moreover, humans worldwide are under threat from diseases that could quickly emerge, such as bird or swine flu, or Ebola hemorrhagic fever; these are primarily animal diseases that under certain circumstances can be transmitted to humans and spread quickly through a population. Thus, microorganisms can still be serious health threats to humans in all parts of the world.

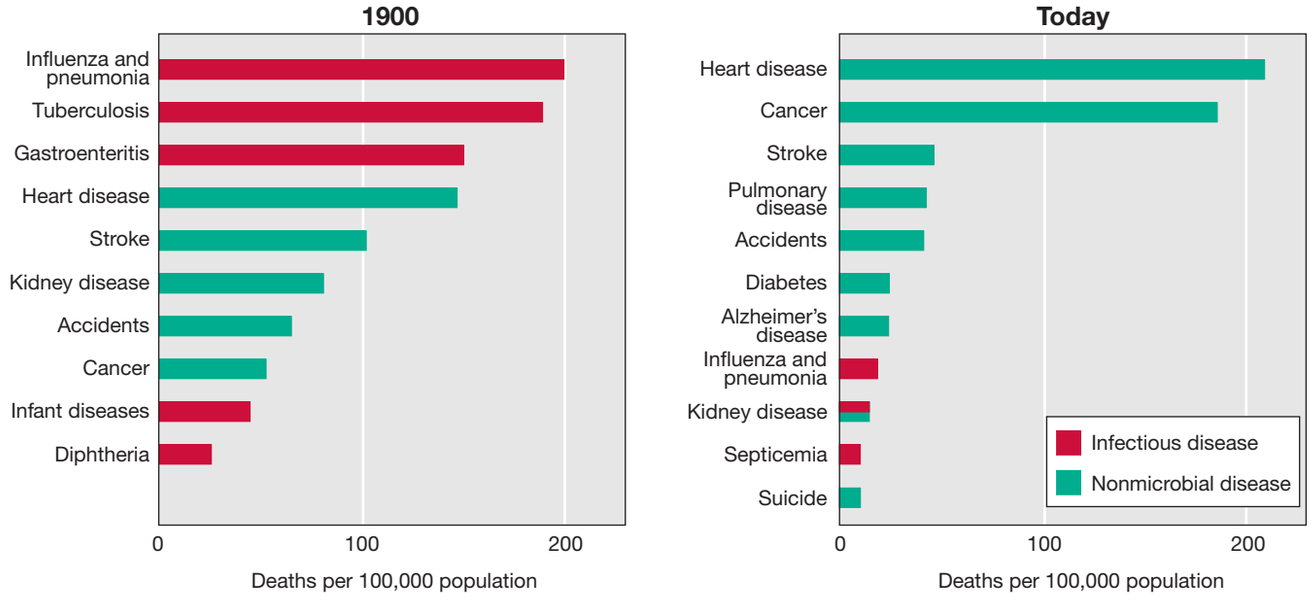

Figure 1.8 Death rates for the leading causes of death in the United States: 1900 and today. Infectious diseases were the leading causes of death in 1900, whereas today they account for relatively few deaths. Kidney diseases can be caused by microbial infections or systemic sources (diabetes, cancers, toxicities, metabolic diseases, etc.). Data are from the United States National Center for Health Statistics and the Centers for Disease Control and Prevention.