JOAN L. SLONCZEWSKI JOHN W. FOSTER

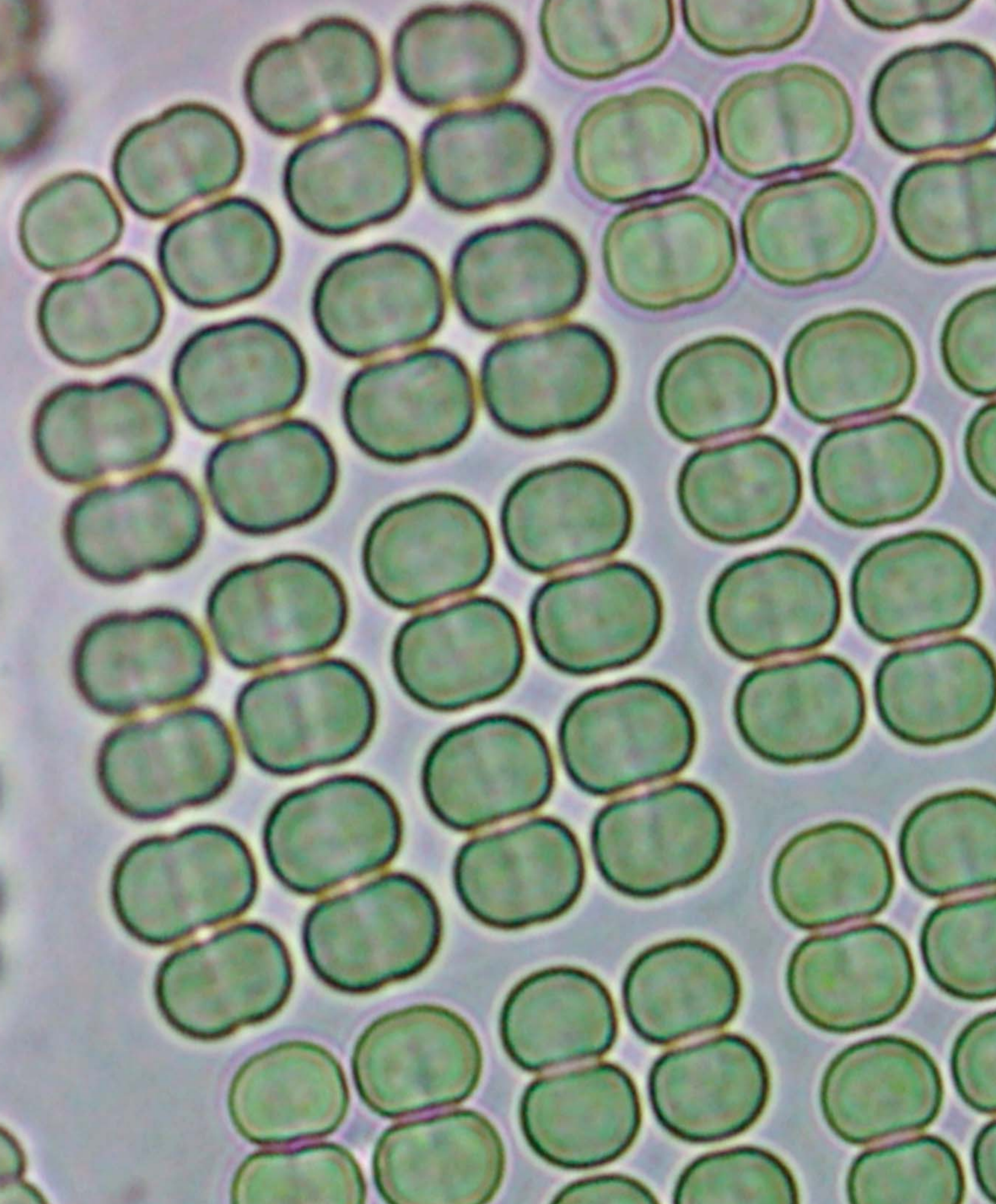
MICRO BIOLOGY

AN EVOLVING SCIENCE 4e

FOURTH EDITION

Microbiology

An Evolving Science



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Microbiology

An Evolving Science

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Dedication

We dedicate this Fourth Edition to the memory of our colleagues, three brilliant scientists and educators: Fred Neidhardt (1931–2016), extraordinary physiologist and founder of the field of microbial stress response; Bob Kadner (1942–2005), renowned microbial physiologist whose discoveries of biosynthesis and transport shaped the field of metabolism; and Katrina Edwards (1968–2014), pioneering geomicrobiologist who founded the Center for Dark Energy Biosphere Investigations (C-DEBI). We, the authors, are grateful for their contributions and deeply moved by their passing.

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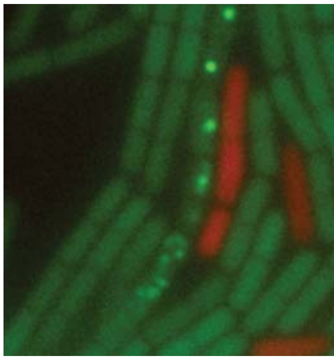

PART 2
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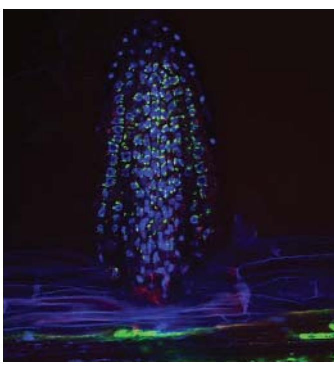

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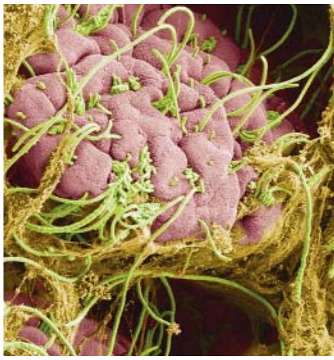

PART 5
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eTOPIC CONTENTS

Access to the eTopics is available through both the ebook and the Norton Coursepack.

PREFACE

Our first three editions established *Microbiology: An Evolving Science* as the defining core text of our generation—the book that inspires undergraduate science majors to embrace the microbial world. This Fourth Edition continues our commitment to the fundamentals, but also highlights two current and breathtaking themes of discovery: Antarctic microbiology and our intestinal microbiome. Antarctic microbes offer models for life on Mars, exotic ecosystems, and opportunities for biotechnology. This new material includes data and images from Joan Slonczewski's own field work in the McMurdo Dry Valleys of Antarctica. Closer to home, our intestinal microbiome reveals extraordinary connections to human health and behavior, as now promoted by the National Microbiome Initiative (NMI). The microbiome story is vividly told by John Foster, a leading investigator of gut bacteria.

In this Fourth Edition, we have maintained our signature balance between cutting-edge ecology and medicine, including the use of case histories in the medical section. Our balanced depiction of women and minority scientists, including young researchers, continues to draw enthusiastic responses from our adopters. Our focus on evolution, and our modern organization reflecting changes in the field, proved so successful that other textbooks have since adjusted their chapter sequence to parallel *Microbiology: An Evolving Science*. We have kept this chapter organization to facilitate year-to-year course transitions for instructors.

In many chapters, we relate topics to current events, to keep students interested in and informed on the role of microbiology in the world today. One example is synthetic biology, the construction of microbes with genetic circuits engineered for commercial use (Chapter 12, Biotechniques and Synthetic Biology). Another example is the use of viral replication cycles to develop lentiviral treatments for cancer and inherited disorders, including the first possible "cure" for pediatric leukemia (presented in Chapter 11, Viral Molecular Biology).

The Fourth Edition still holds to the idea that this text is a community project, drawing not only on the authors' experience as researchers and educators, but also on the input of hundreds of colleagues from around the world to create a comprehensive microbiology book for the twenty-first century. We present the full story of molecular microbiology and microbial ecology from its classical history of Koch, Pasteur, and Winogradsky, right up to the research of twenty-first-century researchers Rita Colwell and Bonnie Bassler. We have included countless contributions recommended by colleagues from around the globe, at institutions such as Washington University, University of California–Davis, University of Wisconsin–Madison, Cornell University, Florida State University, University of Toronto, University of Edinburgh, University of Antwerp, Seoul National University, Chinese University of Hong Kong, and many more. We are grateful to you all.

While we have expanded and developed new topics, we also recognized the need to keep the length and "core" of the book to a size reasonable enough for the undergraduate student. The content in virtually all of the chapters in this book has been limited to a maximum of six numbered sections, helping to keep the coverage from straying too far from the fundamentals. In addition, several chapters underwent major revision in this Fourth Edition, including Chapter 3, Cell Structure and Function, with a tightened opener and a new section on cell aging; and Chapter 21, Microbial Ecology, which opens with a new section on metagenomics and the culturing of "unculturables." Along with these new additions, we have also tightened the content overall, actually decreasing the size of the book from the Third Edition.

In order to contain length while adding new material, we continue to transfer certain topics online as "eTopics." The eTopics are called out in the text, hyperlinked to the ebook, and their key terms are fully indexed in the printed book. Therefore, returning adopters can be confident of keeping access to all of the material they taught from the Second and Third Editions, but now they also have new topics on *Mycobacterium tuberculosis* cell aging and drug resistance (Chapter 3) and on bacteria that convert phage genes into toxin secretion systems (Chapter 25), and much more.

Major Features

Our book targets the science major in biology, microbiology, or biochemistry. Several important features make our book the best text available for undergraduates today:

NEW **Themes of discovery: Antarctic microbiology and our intestinal microbiome.** The Fourth Edition features new content in every chapter on two exciting and relevant new themes. Marginal icons highlight examples of each theme, such as:

- In Chapter 5, research by Asim Bej (University of Alabama Birmingham) and others on psychrophiles reveals the composition and metabolic capabilities of the South Pole microbiome. Novel compounds discovered by members of the polar microbiome have anticancer and antimicrobial potential.
- In Chapter 7, Ruth Lay (Cornell University) used metagenomics to discover that the abundance of some members of the intestinal microbiome are influenced by host genetics. One such organism, *Christensenella minuta,* also influenced weight gain when orally "transplanted" into mouse intestines.

A new "mini-interview" opens each chapter, offering a total of twenty-eight new perspectives from cutting-edge researchers. Examples include:

- A Chapter 1 interview with Dawn Sumner, geomicrobiologist, explaining how cyanobacterial mats colonize Antarctic lakes.
- A Chapter 2 interview with Grant Jensen, whose 3D cryotomography offers an extraordinary view of chlamydia parasitizing a cell.

Research on contemporary themes such as evolution, genomics, metagenomics, molecular genetics, and biotechnology enrich students' understanding of foundational topics and highlight the current state of the field. Every chapter presents numerous current research examples within the up-to-date framework of molecular biology. Examples of current research include tools to explore evolution in aging bacterial colonies; determining the "pangenome," the overall set of genes available to a species; simultaneously profiling gene expression patterns in host and microbe during an infection; and the spectroscopic measurement of carbon flux from microbial communities.

An updated art program with engaging figures that are also dynamic learning tools. Process diagrams have been rendered more accessible by reducing the length of supporting captions and expanding the use of in-figure bubble captions. In addition, scientists pursuing research today are presented alongside the traditional icons of the field. For example, Chapter 1 introduces historical figures such as Koch and Pasteur alongside marine microbiologist Heide Schulz-Vogt and undergraduate students currently conducting experimental evolution of *E. coli*.

Core concepts are presented in a student-friendly way that motivates learning. Ample Thought Questions throughout every chapter challenge students to think critically about core concepts, the way a scientist would.

An innovative media package, including a new Smartwork5 online homework course, provides powerful tools of visualization and assessment. Smartwork5 includes review, critical thinking, visual, and animation questions for every chapter. Each activity builds on the text and pedagogy to help students master key concepts, think critically, and apply what they've learned.

Additional features of the Fourth Edition include:

- **Genetics and genomics are presented as the foundation of microbiology.** Molecular genetics and genomics are thoroughly integrated with core topics throughout the book. This approach gives students an understanding of how genomes reveal potential metabolic pathways in diverse organisms, and how genomics and metagenomics reveal the character of microbial communities.
- **Microbial ecology and medical microbiology receive equal emphasis,** with particular attention paid to the merging of these fields. Throughout the book, phenomena are presented with examples from both ecology and medicine; for example, when discussing horizontal transfer of "genomic islands" we present symbiosis islands associated with nitrogen fixation, as well as pathogenicity islands associated with disease (Chapter 9).
- **Unlike most microbiology textbooks,** our text provides size scale information for nearly every micrograph.
- **Viruses are presented in molecular detail and in ecological perspective.** For example, in marine ecosystems, viruses play key roles in limiting algal populations while selecting for species diversity (Chapter 6). Similarly, a constellation of bacteriophages influences enteric flora.
- **Microbial diversity that students can grasp.** We present microbial diversity in a manageable framework that enables students to grasp the essentials of the most commonly presented taxa, the continual discovery of organisms ranging from anammox bacteria to emerging pathogenic *Escherichia* strains.
- **Appendices for review and further study.** Our book assumes a sophomore-level understanding of introductory biology and chemistry, with on-line eAppendices for those in need of review.

Organization

The topics in this book are arranged so that students can progressively develop an understanding of microbiology from key concepts and research tools. The chapters of Part 1 present key foundational topics: history, visualization, the bacterial cell, microbial growth and control, and virology.

The six chapters in Part 1 present many topics that are then developed in further detail throughout Parts 2 through 5. Part 2 presents modern genetics and genomics. Part 3 presents cell metabolism and biochemistry, although the chapters in Part 3 are written in such a way that they can be presented before the genetics material if so desired. Part 4 explores microbial ecology and diversity and discusses the roles of microbial communities in local ecosystems and global cycling. And then the chapters of Part 5 (Chapters 23–28) present medical and disease microbiology from an investigative perspective, founded on the principles of genetics, metabolism, and microbial ecology.

What's New in the Fourth Edition?

Throughout the Fourth Edition of *Microbiology: An Emerging Science*, research examples have been updated to highlight the newest experimental techniques and important topics of interest in microbiology today, including current examples of the two new themes—Antarctic microbiology and the intestinal microbiome. The content in each chapter has been focused around fewer numbered chapter sections to help students master the fundamentals. The art has been updated and numerous Thought Questions and Special Topic boxes have been updated. Every chapter opens with a new research interview that features the work of established scientists, postdocs, and graduate students from around the world. A review of of these changes by chapter are featured in the following list.

CHAPTER 1: Microbial Life: Origin and Discovery. The chapter opener describes research on cyanobacterial mats that grow at the bottom of Antarctic lakes. Other new and unusual microbes are presented, including *Pyrodictium abyssi*, which lives off of the sulfides spewed from oceanic thermal vents, and the giant marine bacterium, *Thiomargarita namibiensis*.

CHAPTER 2: Observing the Microbial Cell. In the chapter opener, pathogenic chlamydias are seen in a whole new light—using 3D cryotomographic microscopy. Exciting imaging techniques that continue to push forward our understanding of cell behavior are presented. Super resolution imaging enables single molecules to be tracked within living cells, and a new special topic on NanoSIMS (nanoscale secondary ion mass spectrometry) describes how this chemical imaging method is being used to probe intestinal microbiomes.

CHAPTER 3: Cell Structure and Function. The molecular processes that coordinate DNA replication and cell division are the subject of the chapter opener. Several microbial cell biology topics are expanded and updated, including cell fractionation, a discussion of the cell envelope, and polar aging.

CHAPTER 4: Bacterial Culture, Growth, and Development. The chapter opener reveals the microbial diversity and evolution occurring in old bacterial colonies. The explanation of generation time and the description of continuous culture is revised for clarity. Recent research alters our view of what's going on during stationary phase within a liquid culture. A new special topic follows antibiotic hunters as they search for new medicines among "unculturable" microorganisms. New data on biofilm-busting peptides are presented.

CHAPTER 5: Environmental Influences and Control of Microbial Growth. Interspecies cell signaling is discussed in the chapter opener. The impacts of human activities, including global climate change, on microbial ecosystems are updated with some of the latest research. A new special topic looks at bacteriophage therapy to treat biofilm infections.

CHAPTER 6: Viruses. This first of two chapters on viruses opens with viral ecology, to highlight the critical roles that viruses play in ecosystems. Gut Bacteriophages in the gut microbiome is the topic of Section 6.4. The modern use of genome sequencing to classify viruses is presented. A special topic presents research on the role of a recently identified virus that confers thermotolerance to both its host fungus and the fungi's symbiotic plant host.

CHAPTER 7: Genomes and Chromosomes. The chapter opener describes research using molecular biology and fluorescence cell imaging to follow the fate of plasmids and the chromosome in *E. coli*. Section 7.5 is expanded to include the latest information about archaeal chromosomes. New data is included about intestinal metagenomics and single-cell genomics. A new special topic describes the molecular mechanisms that keep sister chromosomes from being severed by the growing septum during bacterial cell division.

CHAPTER 8: Transcription, Translation, and Bioinformatics. The chapter opener presents current research on the structural biology of coupled transcription and translation in bacteria. Much of the chapter is revised. Discussion of bioinformatics is revised extensively, including new material on how bioinformatics is revealing the complex interactions within the human gut microbiome. The processes of transcription, translation, and transertion are described using new research examples and art that makes translation more realistic and easier to understand. A new special topic looks at new discoveries on the structural biology of ribosome translocation during protein synthesis.

CHAPTER 9: Gene Transfer, Mutations, and Genome Evolution. The selection pressure of antibiotics on *Streptococcus pneumoniae* evolution is discussed in the chapter opener. Information on CRISPR is updated with new examples to emphasize its growing utility in molecular biology research. The discussion of horizontal gene transfer includes new data from studies on Antarctic microbes and on movement of genes between bacteria and eukaryotes. A new special topic on studies of DNA repair proteins containing [4Fe-4S] clusters hypothesizes that these proteins use electrons to locate damaged DNA.

CHAPTER 10: Molecular Regulation. A new chapter opener looks at how enterohemorrhagic *E. coli* virulence genes are regulated. The roles of RNA thermometers in the heat-shock response and of riboswitches in regulating gene expression are introduced. Discussion of the class of regulatory RNA molecules known as small RNA (sRNA) is updated and expanded with numerous examples, including sRNAs in Archaea that have counterparts in both Eukarya and Bacteria.

CHAPTER 11: Viral Molecular Biology. This chapter on viruses is extensively revised. It opens with current research on the presence of endogenous retroviral particles that are expressed in human embryos. The section on bacteriophage uses lambda phage as the model organism, and includes examples from genome analysis and synthetic biology to highlight contemporary approaches to understanding its role in the human gut microbiome. New images using cryo-electron tomography illustrate in great detail the organization of RNA within an influenza virion. The exciting antitumor tool, T-VEC, an engineered HSV-1 virus, is described.

CHAPTER 12: Biotechniques and Synthetic Biology. The chapter opener introduces Ribo-T, an engineered ribosome, which highlights some of the possibilities of biomolecular engineering and synthetic biology. The use of the CRISPR/Cas9 system as an editing tool and method of regulating gene expression in experiments is described. The idea of using synthetic auxotrophy as a biocontainment method for engineered *E. coli* (and potentially other microbes) is described.

CHAPTER 13: Energetics and Catabolism. The gut microbiome is featured in a new chapter opener, which describes how *Bacteroides* species in the human intestines secrete catabolic enzymes, thus providing essential catabolites for many microbial species in the gut. New research from Antarctica is presented on psychotrophs that metabolism phenanthrene.

CHAPTER 14: Electron Flow in Organotrophy, Lithotrophy, and Phototrophy. A new chapter opener describes extracellular electron transfer among *Geobacter* species—a form of microbial electricity. In the gut, *Salmonella enterica* subvert neutrophils by using tetrathionate to assist in pathogenesis. A new special topic surveys our attempts to harness microbial electricity to power our electrical devices.

CHAPTER 15: Biosynthesis. The chapter opener highlights a simple assay for screening soil-dwelling actinomycetes that produce novel glycopeptide antibiotics. The discussion of ways in which microbes control the energetic costs of biosynthesis is expanded to include recently discovered examples of resource sharing within Antarctic marine phototrophs and among *E. coli* that form nanotubes to exchange amino acids.

CHAPTER 16: Food and Industrial Microbiology. A novel lipase isolated from an Antarctic psychrophile, *Candida antarctica*, is the subject of the new chapter opener. The discovery of microbial biologicals and their commercialization is featured. For example, bioprospecting identified a biological fungicide, whose active ingredient is *Streptomyces lydicus*, which suppresses fungi that attack plant roots and leaves.

CHAPTER 17: Origins and Evolution. A new chapter opener presents evidence of competitive and cooperative evolution in *E. coli*. Some of the latest data from Richard Lenski's long-term evolution experiment is included. The chapter presents recent clues to the nature of early life that are found in the Dry Valleys of Antarctica, where cyanobacteria form thick microbial mats. The criteria for defining a species is updated to include current information from genome and rRNA analysis along with ecotype sharing.

CHAPTER 18: Bacterial Diversity. The chapter opener presents fascinating data about the biofilms found growing on colorectal tumors. Information has been updated about the mosaicism of deep-branching thermophile genomes from Aquificae and Thermotogae. A new special topic introduces bizarre looking filamentous bacteria that form symbiotic relationships with cells in the mammalian gut.

CHAPTER 19: Archaeal Diversity. Our understanding of the Archaeal world continues to change rapidly. The chapter opener describes *Altiarchaeum hamiconexum*, a marsh-dwelling archaeon that uses its grappling hook appendages to link together into biofilms. The latest updates on archaeal phylogeny are included, like reclassification of the Miscellaneous Crenarchaeota Group to the Bathyarchaeota. Examples of ammonia-oxidizing archaea are discussed, including the deep ocean psychrophile, *Cenarchaeum symbiosum*, which is an endosymbiont of a marine sponge. A new special topic looks at current research on methanogens living in our intestines and what factors cause them to colonize some hosts, but not others.

CHAPTER 20: Eukaryotic Diversity. A new chapter opener discusses choanoflagellates from Antarctica that cycle between single-cell and colonial forms. Cellular and genetic traits of these protists make them an excellent organism for the study of metazoan origins. Recent data is described about inducing multicellularity in the green algae, *Chlamydomonas reinhardtii*. The lineup of parasitic protozoa discussed in the chapter is expanded to include a number of intestinal parasites, like *Cryptosporidium parvum*, *Balantidium coli*, and *Encephalitozoon intestinalis*.

CHAPTER 21: Microbial Ecology. The chapter opener gets "crabby." It describes the symbiotic relationship between chemosynthetic bacteria and the yeti crab at hydrothermal vents located 2.5 miles down beneath the surface of the Antarctic Southern Ocean. This chapter is extensively reorganized and updated with new material on metagenome sequencing, a new discussion on the human colonic microbiome's roles in host digestion, brain health and immunity, and recent research findings on oceanic microbes, like *Prochlorococcus*. A new special topic presents results of studying the ecology and migration of cyanobacterial mats found in many Antarctic lakes.

CHAPTER 22: Microbes in Global Elemental Cycles. The discovery of *Nitrospira* species that perform both ammonia and nitrite oxidation is presented in the chapter opener. The special topic presents evidence that a million-year-old underground river carrying iron and sulfur bacteria courses 500 meters below the Taylor Valley in Antarctica. The chapter presents recent scientific modeling data, which cautions that global warming is increasing microbial activity in the once frozen permafrost. Release of carbon stores from the permafrost due to microbial metabolism could accelerate global warming.

CHAPTER 23: Human Microbiota and Innate Immunity. The new chapter opener presents cryo-electron microscopy data illustrating the assembly of the multiprotein inflammasome complex. This chapter is thoroughly reorganized with updated presentations of innate immunity and a new emphasis on the human body as an ecosystem. In particular, Section 23.2 focuses on the gut microbiota, presenting numerous examples of beneficial gut microbes and introducing the concept of dysbiosis, the accidental penetration of organisms beyond a site of colonization or an imbalance in microbiome composition.

CHAPTER 24: The Adaptive Immune Response. The chapter opener shows how bystander B cells in lymph nodes are essential for T cell migration, an essential early step in B cell maturation into a plasma cell. This chapter is extensively reorganized. Sections on antibody structure and production are merged and streamlined. There is a new section on gut mucosal immunity. A discussion about vaccinations has been moved into this chapter from Chapter 26. A new special topic provides evidence that endogenous retroviruses may help B cells respond to the presence of T cell-independent antigens.

CHAPTER 25: Microbial Pathogenesis. A new chapter opener looks at recent experimental results that reveal how *Yersinia pestis* co-opts host proteins to aid in its pathogenesis. The molecular mechanisms of other pathogenic microbes are presented, such as, the role of the adhesin molecule MAM7 in initiating contact between a Gram-negative pathogen and its host cell. New information is presented on how pathogens control virulence factor gene expression based on their environment and how they thwart antigen presentation by the host immune system. The section on experimental tools used to study pathogenesis is completely rewritten. It now focuses on the current methods in genomic sequencing and bioinformatics analysis, transcriptomics, and imaging and fluorescent probe techniques to address cell biological questions.

CHAPTER 26: Microbial Diseases. The chapter opener summarizes current facts about Zika virus, reminding us that emerging infectious diseases are still a serious threat to human health. Information about numerous examples of microbial disease have been updated, including a new discussion of osteomyelitis, updates on the virulence factors and molecular mechanisms of infection used by *Helicobacter pylori*, and a new discussion of diarrhea and its impacts on the gut microbiome.

CHAPTER 27: Antimicrobial Therapy. Antimicrobial hunters and their treasures are the subject of the new chapter opener. In this example, an Antarctic sponge is the source of darwinolide, a novel diterpene that is effective against MRSA. New technologies are presented that could be used for rapid identification of pathogens in the clinical laboratory, such as multiplex PCR and miniaturized magnetic resonance machines. A new special topic looks at the use of monoclonal antibodies as antimicrobials.

CHAPTER 28: Clinical Microbiology and Epidemiology. The new chapter opener looks at novel genome-based tests to profile the gut microbiome in patients and correlate the profile with various gastrointestinal diseases. Updates on rapid and automated clinical detection methods are described, including the use of next-gen sequencing and programmable RNA sensors to identify pathogens in patient samples. The section on detecting emerging infectious diseases is completely rewritten. It now includes discussions of Zika virus and the role of climate change on the emergence and spread of microbial diseases.

Resources

SMARTWORK5 ONLINE HOMEWORK. Norton's powerful and accessible online homework platform features answer specific feedback, a variety of engaging question types, and the integration of the stunning art from the book and process animations to help students master microbiology concepts. Smartwork5 integrates with campus LMS's such as Blackboard and Canvas and features a simple, intuitive interface making it the easiest-to-use online homework system for instructors and students.

PRESENTATION TOOLS. Every figure and photograph in the textbook is available in JPEG and PowerPoint format for use in lecture. In order to provide stunning, high-quality visuals, every image has been hand-examined to make sure colors will not fade when projected and to optimize font size and composition for clear, legible viewing even in the back row. Labeled and unlabeled versions are available. In addition, Lecture PowerPoint decks including key figures form the text, links to animations, and clicker questions, are available for download at wwnorton.com/instructors.

MICROGRAPH DATABASE. The Micrograph Database includes searchable access to most of the micrographs in the textbook, tagged by characteristics such as taxonomy, shape, and habitat. The Micrograph Database can be accessed at wwnorton.com/instructors.

PROCESS ANIMATIONS. Sixty process animations depicting key processes of microbiology are offered in multiple formats and and embedded in PowerPoint files. These animations are all based on the art found in the textbook and were developed under the careful supervision of the textbook authors. Student access to the animations is available in the ebook, Smartwork5 online homework course or via the Coursepack. Instructor access to the process animations is available at wwnorton.com/instructors.

Animation Topics Include:

Microscopy
Replisome Movement in a Dividing Cell
Chemotaxis
Phosphotransferase System (PTS) Transport
Dilution Streaking Technique
Biofilm Formation
Endospore Formation
Lysis and Lysogeny
Supercoiling and Topoisomerases
DNA Replication
Rolling Circle Mechanism of Plasmid Replication
PCR
Protein Synthesis
Protein Export
SecA-Dependent General Secretion Pathway
ABC Transporters
Bacterial Conjugation
Recombination
DNA Repair Mechanisms: Methyl Mismatch Repair
DNA Repair Mechanisms: Nucleotide Excision Repair
DNA Repair Mechanisms: Base Excision Repair
Transposition
The *lac* Operon
Transcriptional Attenuation
Chemotaxis: Molecular Events
Quorum Sensing
Influenza Virus Entry into a Cell
Influenza Virus Replication
HIV Replication
Herpes Virus Replication
Construction of a Gene Therapy Vector
Tagging Proteins for Easy Purification
Real-Time PCR
A Bacterial Electron Transport System
ATP Synthase Mechanism
Oxygenic Photosynthesis
Agrobacterium: A Plant Gene Transfer Vector
Phylogenetic Trees
DNA Shuffling
Listeria Infection
Light-Driven Pumps and Sensors
Malaria: A Cycle of Transmission between Mosquito and Human
The Basic Inflammatory Response
Phagocytosis
The Activation of the Humoral and Cell-Mediated Pathways
Cholera Toxin Mode of Action
Process of Type III Secretion
Retrograde Movement of Tetanus Toxin to an Inhibitory Neuron
DNA Sequencing

TEST BANK. Thoroughly revised for the Fourth Edition and using the Norton Assessment Guidelines, each chapter of the Test Bank consists of five question types classified according to the first five levels of Bloom's taxonomy of knowledge types: Remembering, Understanding, Applying, Analyzing, and Evaluating. Questions are further classified by section and difficulty, making it easy to construct tests and quizzes that are meaningful and diagnostic according to instructors' needs. Questions are multiple-choice and short-answer. The Test Bank is available in *ExamView Assessment Suite*, Word RTF, and PDF formats, downloadable from wwnorton.com/instructors.

COURSEPACKS. At no cost to professors or students, Norton Coursepacks are available in a variety of formats, including all versions of Blackboard and WebCT. With just a simple download, an adopter can bring high-quality Norton digital media into a new or existing online course (no extra student passwords required), and it's theirs to keep. Content includes chapter-based assignments, quizzes, animation activities and more. Coursepacks can be downloaded at wwnorton.com/instructors.

ENHANCED EBOOK. An affordable and convenient alternative to the print book, Norton Ebooks retain the content and design of the print book and allow students to highlight and take notes, print chapters as needed, and search the text with ease. The enhanced ebook includes:

- **Process animations** based on the text art and developed under the watchful eyes of the textbook authors.
- **Links to eTopics** written by Joan Slonczewski and John Foster, which supplement and enrich concepts covered in the text.
- **Flashcards** of all the key terms in the book and their definitions.

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Fourth Edition Reviewers

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To the Reader: Thanks!

We greatly appreciate your selection of this book as your introduction to the science of microbiology. As our textbook continues to evolve, it benefits greatly from the input of its many readers, students as well as professors. We truly welcome your comments, especially if you find text or figures that are in error or unclear. Feel free to contact us at the addresses listed below.

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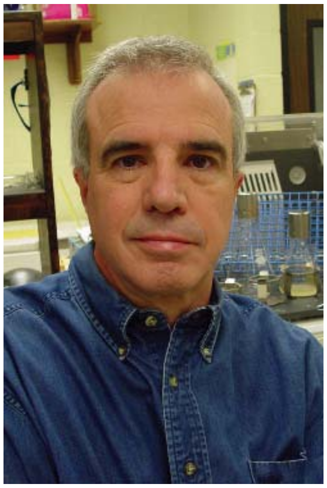

CHAPTER 1

Microbial Life: Origin and Discovery

Microbes grow in frozen Antarctica, and everywhere else. A human body contains many more microbes than it does human cells, including 100 trillion bacteria in the digestive tract. Throughout history, humans had a hidden partnership with microbes ranging from food production to mining minerals. Microscopes revealed the tiny organisms at work in our bodies and in our environment. In the twentieth century, microbial genetics led to recombinant DNA and sequenced genomes. Today, microbes lead discoveries in medicine and global ecology.

CURRENT RESEARCH highlight

Cyanobacterial mats under ice. At the bottom of an Antarctic lake, beneath 3 meters of ice, cyanobacteria capture enough light for photosynthesis. The cyanobacteria grow flame-shaped pinnacles that produce oxygen gas. Protists and other microscopic consumers flourish in a complex ecosystem, at temperatures just above freezing. They survive dark winters while surrounding environments are frozen to −80°C. Their existence suggests the possibility of nearly frozen life on other planets, such as Mars.

Source: Ian Hawes et al. 2013. *Biology* **2**:151.

DAWN SUMNER AND DALE ANDERSEN

AN INTERVIEW WITH

DAWN SUMNER, GEOMICROBIOLOGIST, UC DAVIS

COURTESY OF DAWN Y. SUMNER

How does your study of microbes extend the work of historic Antarctic explorers?

Our work in Antarctic lakes expands our knowledge of the most biologically productive ecosystems in the Antarctic Dry Valleys. Early explorers recognized microbial growth in shallow ponds and streams but didn't have access to the luxuriant mats that coat the lake floors until diving started in the 1980s. We now use modern molecular and computational approaches to better understand how these communities have adapted to the extreme seasonal changes of the lake environments.

What might Antarctic microbes suggest about potential life on Mars?

The widespread distribution of cyanobacterial mat organisms shows that they can be transported by wind and survive freeze-drying. These mats provide an excellent model for life on Earth prior to the evolution of macroscopic grazers and burrowers, as well as for possible ecologies on other planets, such as Mars. Mars transitioned from a planet with flowing liquid water to one dominated by ice, and during this transition, ice-covered lakes were likely common.

Life began early in the history of planet Earth, with microscopic organisms, or "microbes." Over the eons, those microbes evolved to shape our atmosphere, our geology, and the energy cycles of all ecosystems. For the first 2 billion years, all life was microbial. What did it look like? To imagine it, we can look at the parts of the world that still support only microscopic life, such as the McMurdo Dry Valleys of Antarctica (**Fig. 1.1**). In summer, the temperature rarely rises above freezing, while in winter it plunges below −60°C. The only native life-forms are bacteria, lichens and protists, and tiny invertebrates such as nematodes. Cyanobacteria form thick mats below the ice of frozen lakes, where they support microscopic ecosystems (see the Current Research Highlight). Remarkably, some cyanobacterial mats can survive for years trapped in ice, to emerge when dry winds sublime the surface (**Fig. 1.1** inset). The emerging microbes blow away and colonize new habitats.

Could Antarctic microbiology help us find life on other planets? The Dry Valleys are the closest model we have to what life might look like on Mars (see **Special Topic 1.1**). As of this writing, the existence of microbial life on Mars is still unknown, but here on Earth, many terrestrial microbes remain as mysterious as Mars. Barely 0.1% of the microbes in our biosphere can be cultured in the laboratory; even the digestive tract of a newborn infant contains species of bacteria unknown to science.

We find microbes throughout our biosphere, from the superheated black smoker vents at the ocean floor to the interiors of our own bodies. Bacteria such as *Escherichia coli* are among the 100 trillion inhabitants of our intestines, where they help digest our food. Alternatively, *E. coli* may colonize the plants we eat (**Fig. 1.2A**). Microbial eukaryotes (cells with nuclei) such as the voracious *Stentor* engulf aquatic prey (**Fig. 1.2B**). Archaea are a life-form distinct from both bacteria and eukaryotes. Some archaea grow in extreme environments, such as concentrated salt (**Fig. 1.2C**). And all kinds of life host viruses. For example, herpes simplex virus infects human cells (**Fig. 1.2D**).

Yet before we devised microscopes in the seventeenth century, we humans were unaware of the unseen living organisms that surround us, that float in our air and water, and that inhabit our own bodies. Microbes generate the very air we breathe, including nitrogen gas and much of the oxygen and carbon dioxide. They fix nitrogen for plants, and they make vitamins, such as vitamin B_{12}. In the ocean, microbes produce biomass for the food web that feeds the fish we eat, and microbes consume toxic wastes such as the oil from the *Deepwater Horizon* spill in the Gulf of Mexico in 2010. At the same time, virulent pathogens take our lives—and researchers risk their lives to study them. Working with pathogens such as Ebola virus requires sealed suits and respiratory equipment (**Fig. 1.3**). Despite all

FIGURE 1.1 ■ **Antarctic "Dry Valleys," where all native life is microbial.** Surface temperatures range from 0°C (summer) to −40°C (winter). **Inset:** A cyanobacterial mat emerges from the ice.

JOAN SLONCZEWSKI AND RACHAEL MORGAN-KISS, NSF

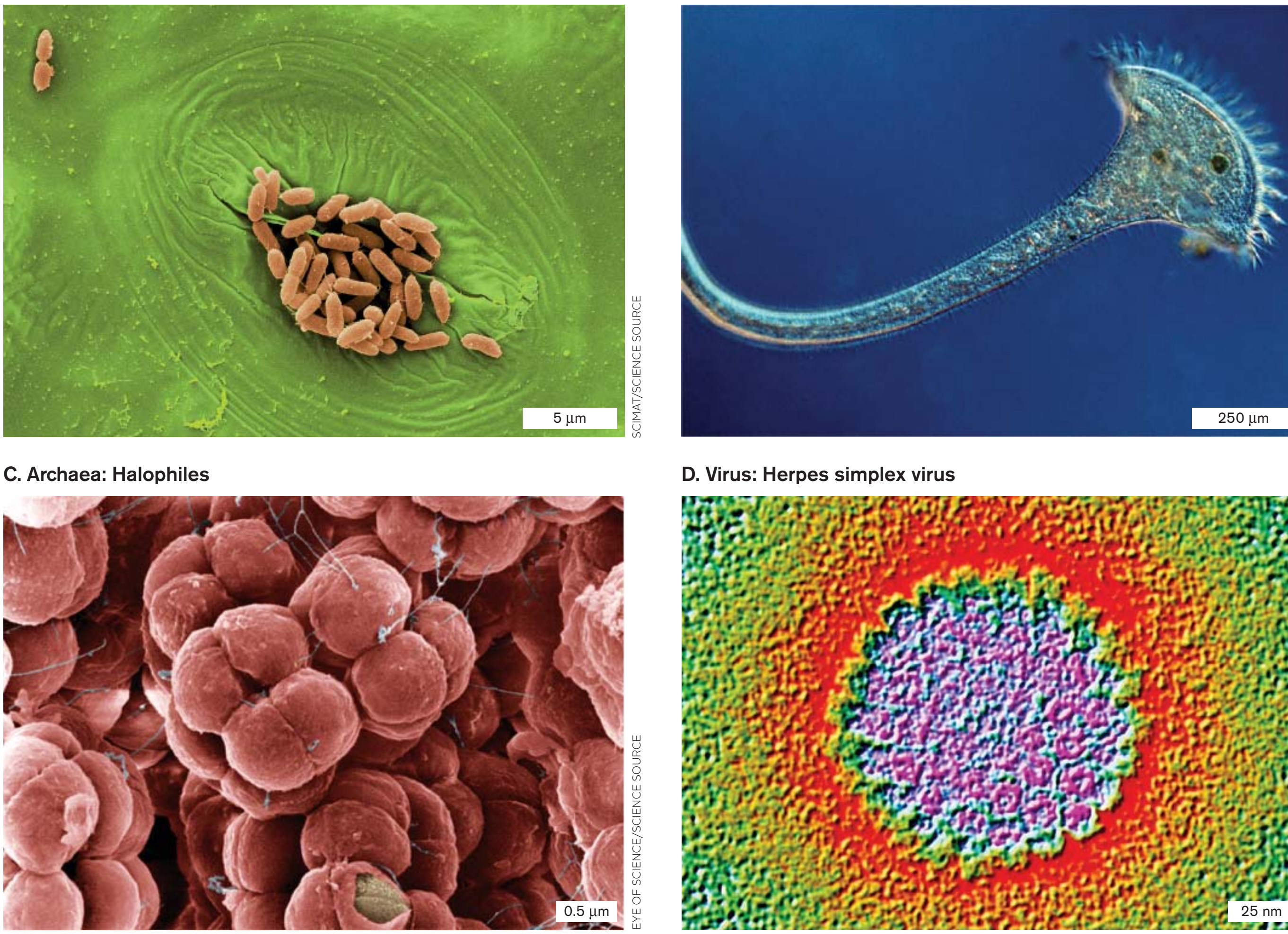

FIGURE 1.2 ■ **Representative kinds of microbes.** **A.** Bacteria: *E. coli* on leaf stomate. **B.** Eukaryote: *Stentor*. **C.** Archaea: Halococcus. **D.** Virus: Herpes simplex virus.

FIGURE 1.3 ■ **Researching deadly pathogens.** This laboratory in Lyon, France, studies Ebola virus and influenza virus.

our advances in medicine and public health, humans continue to die of microbial diseases. Each year, millions of children succumb to waterborne pathogens and respiratory infections.

Today we discover surprising new kinds of microbes in places they were previously thought absent, such as 3 kilometers down in a South African gold mine, or within human breast milk. Microbes shape our biosphere and provide new tools that impact human society. For example, the use of heat-stable bacterial DNA polymerase (a DNA-replicating enzyme) in a technique called the **polymerase chain reaction** (**PCR**) allows us to detect minute amounts of DNA in traces of blood or fossil bone. Microbial technologies led us from the discovery of the double helix to the sequence of the human genome, the total genetic information that defines our species.

In Chapter 1 we introduce the concept of a microbe, and we survey the history of human discovery. We explain how to show which pathogen causes a disease.

SPECIAL TOPIC 1.1 How Did Life Originate?

If all life on Earth shares descent from a microbial ancestor, how did the first microbe arise? The earliest fossil evidence of cells in the geological record appears in sedimentary rock that formed as long ago as 3.8 billion years. Although the nature of the earliest reported fossils remains controversial, it is generally accepted that "microfossils" from over 2 billion years ago were formed by living cells. Moreover, the living cells that formed these microfossils looked remarkably similar to bacterial cells today, forming chains of simple rods or spheres (**Fig. 1**).

The exact composition of the first environment for life is controversial. The components of the first living cells may have formed from spontaneous reactions sparked by ultraviolet absorption or electrical discharge. American chemists Stanley Miller (1930–2007) and Harold C. Urey (1893–1981) argued that the environment of early Earth contained mainly reduced compounds—compounds that have a strong tendency to donate electrons, such as ferrous iron, methane, and ammonia. More recent evidence has modified this view, but it is agreed that the strong electron acceptor oxygen gas (O_2) was absent until the first photosynthetic microbes produced it. Today, all our cells are composed of highly reduced molecules that are readily oxidized (lose electrons to O_2). This seemingly hazardous composition may reflect our cellular origin in the chemically reduced environment of early Earth.

In 1953, Miller attempted to simulate the highly reduced conditions of early Earth to test whether ultraviolet absorption or electrical discharge could cause reactions producing the fundamental components of life (**Fig. 2A**). He boiled a solution of water containing hydrogen gas, methane, and ammonia and applied an electrical discharge (comparable to a lightning strike). The electrical discharge excites electrons in the molecules and causes them to react. Astonishingly, the reaction produced a number of amino acids, including glycine, alanine, and aspartic acid. A similar experiment in 1961 by Spanish-American researcher Juan Oró (1923–2004) (**Fig. 2B**) combined hydrogen cyanide and ammonia under electrical discharge to obtain adenine, a fundamental component of DNA and of the energy carrier adenosine triphosphate (ATP).

Molecules that spontaneously formed in Miller's and Oró's experiments are also found in meteorites and comets. This observation led Oró to propose that the first chemicals of life could have come from outer space, perhaps carried by comets. Furthermore, at the time life arose on Earth, Earth's geochemistry resembled that of other planets, such as Mars. Could Mars, too, have originated life?

In 2012, to seek evidence for life on Mars, NASA landed the *Mars Science Laboratory*, or *Curiosity* rover, near the base of a mountain on the planet Mars. The car-sized rover had a laser to drill into rock, X-ray and fluorescence analyzers, and camera microscopes. It began its mission to test the Martian soil

FIGURE 1 ▪ Microfossils of ancient cyanobacteria. These fossils, from the Bitter Springs Formation, Australia, are about 850 million years old.

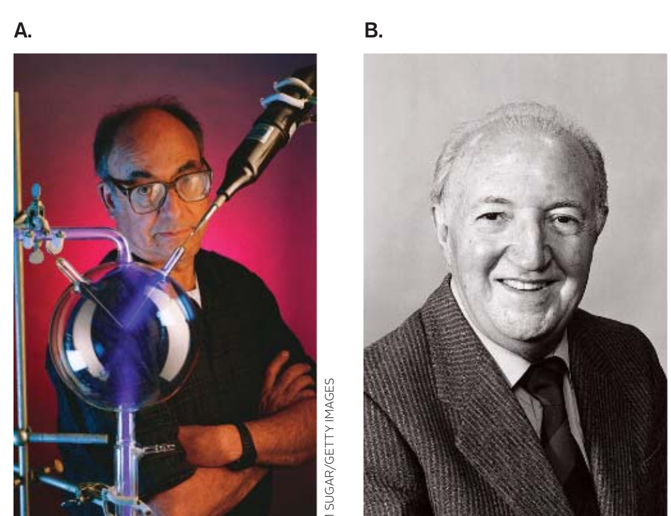

FIGURE 2 ▪ Simulating early Earth's chemistry. **A.** Stanley Miller with the apparatus of his early-Earth simulation experiment. **B.** Biochemist Juan Oró demonstrated the formation of adenine and other biochemicals from reaction conditions found in comets.

for water, organic compounds, and other potential evidence of microbial life.

Among the most fascinating bits of evidence to come back from Mars were the photographs of rock formations dating to 3.7 billion years ago, near the time we believe life began on Earth (**Fig. 3**). Geologist Nora Noffke, at Old Dominion University, examined these photographs using the same criteria geologists use to define microfossils of early life on Earth. She observed many features of Martian rock that resemble ancient terrestrial fossils of microbial mats—possibly cyanobacteria similar to those of Antarctic lakes. For example, flat stretches of sediment show layers that appear folded or even rolled up, as if a flexible mat of living cells had torn and rolled back onto itself. Noffke compiled such a large group of features that ultimately, she argues, if such forms indicate fossil life on Earth, they must also indicate fossil life on Mars.

If microbial life once existed on Mars, could some forms live on, perhaps under the rock strata where pockets of water remain? As of this writing, *Curiosity's* quest for data rolls on.

RESEARCH QUESTION

How can we be sure that a fossil formation arose biogenically—that is, from a life-form? Could you define quantitative criteria for microbial fossils?

Noffke, Nora. 2015. Ancient sedimentary structures in the <3.7 Ga Gillespie Lake Member, Mars, that resemble macroscopic morphology, spatial associations, and temporal succession in terrestrial microbialites. *Astrobiology* **15**:169–192.

B.

A.

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FIGURE 3 ■ Mars fossil life. A. Sedimentary formations on Mars resemble those of fossil cyanobacterial mats on Earth. **Inset:** *Curiosity* rover (shown in this artist's depiction) took the photograph. **B.** Nora Noffke argues that the Mars formations are microbially induced sedimentary structures, comparable to those found on Earth.