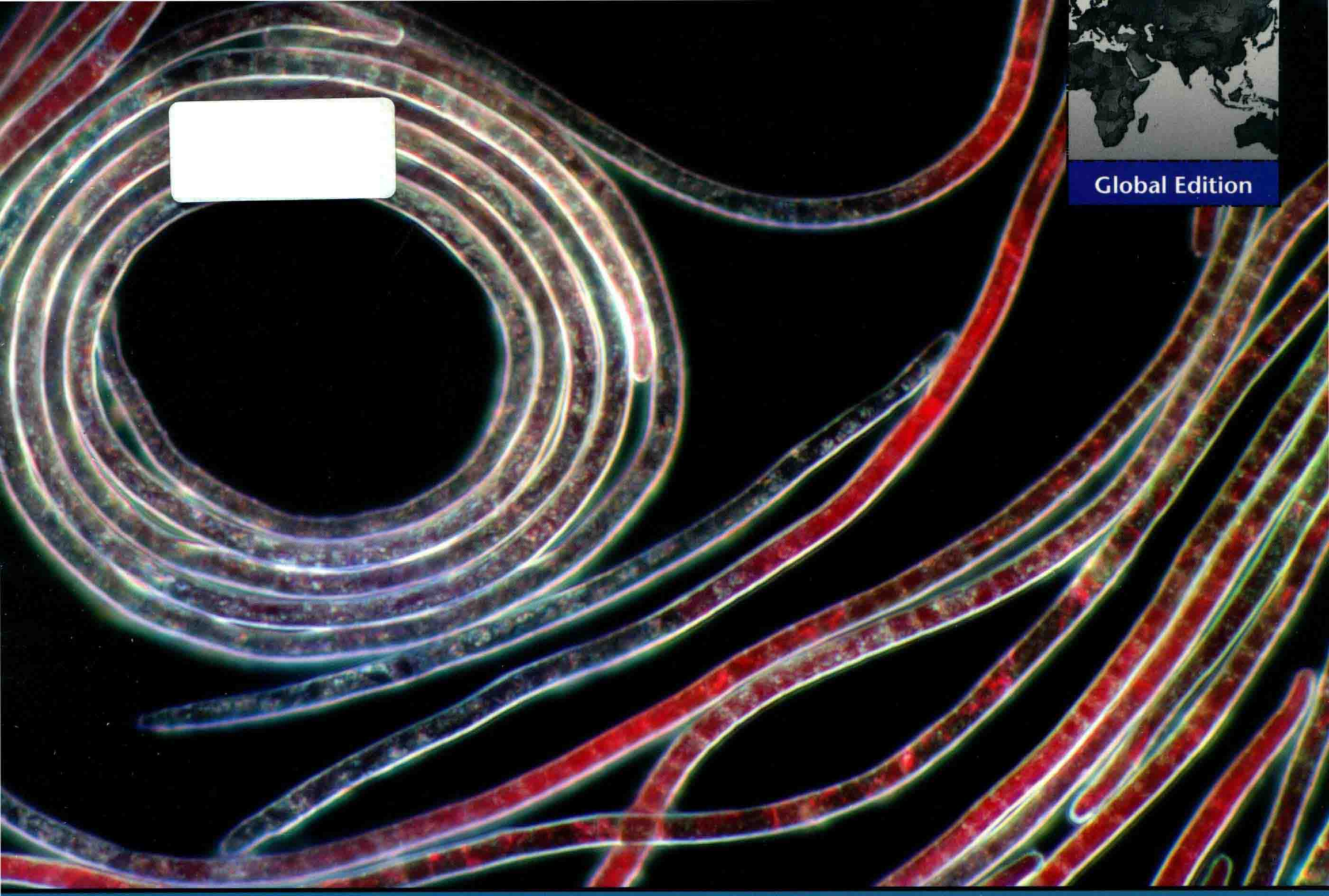

Global Edition

Brock Biology of Microorganisms

Thirteenth Edition

PEARSON

Michael Madigan • John Martinko • David Stahl • David Clark

This Global Edition includes enhancements making it more relevant to students outside the United States.

Brock Biology of Microorganisms, **Global Edition continues to set the standard for impeccable scholarship, accuracy, and outstanding illustrations and photos.**

New material in the Global Edition:

- **New Global Microbial Sidebars** — richly illustrated vignettes presenting interesting topical material related to a chapter's central theme. This edition includes new sidebars from global contributors.
- **New co-author Dave Stahl** brings his unique expertise to the book by expanding and updating the Microbial Ecology coverage and writing a brand new chapter on Symbiosis (Chapter 25).
- **Completely revised overview chapter on Immunology** (Chapter 28).
- **New Big Ideas sections** at the end of each chapter review the core principles in the chapter by summarizing each section in 2–3 sentences.

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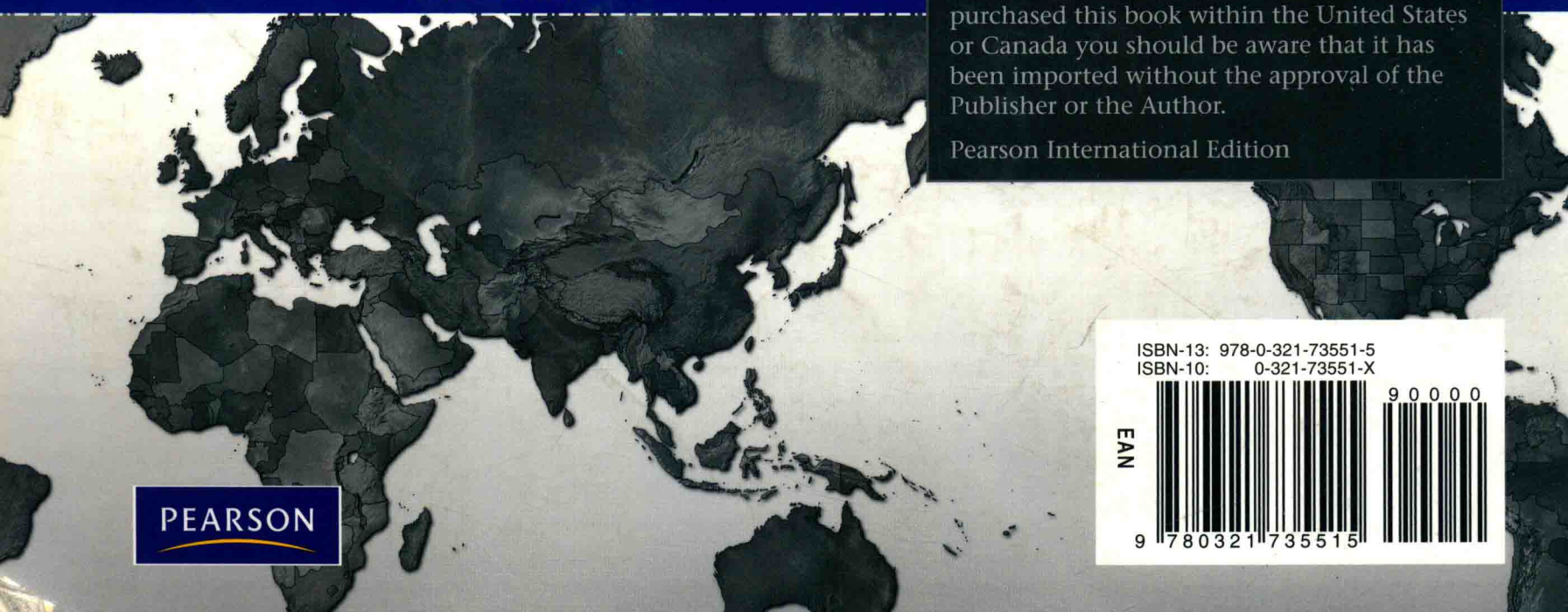

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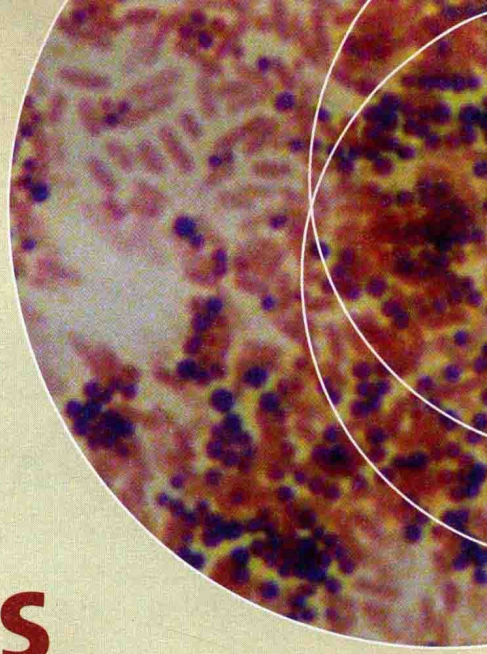

Brock

Biology of Microorganisms

Global Edition

Thirteenth Edition

Michael T. Madigan
Southern Illinois University Carbondale

John M. Martinko
Southern Illinois University Carbondale

David A. Stahl
University of Washington Seattle

David P. Clark
Southern Illinois University Carbondale

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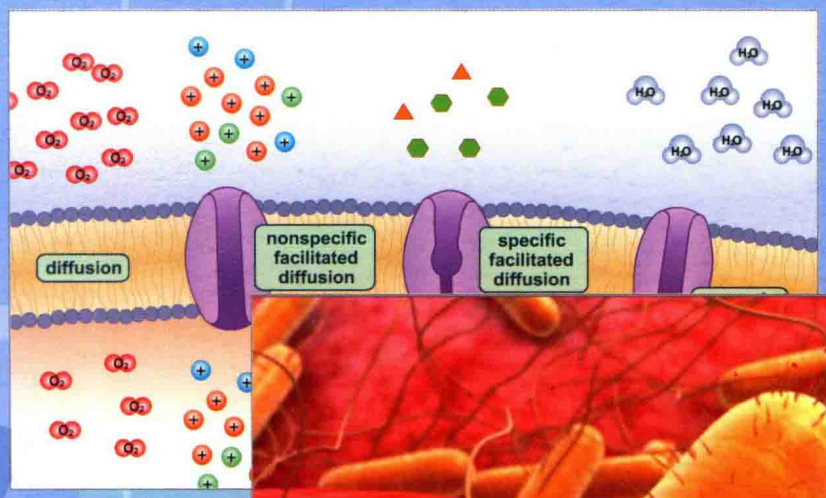

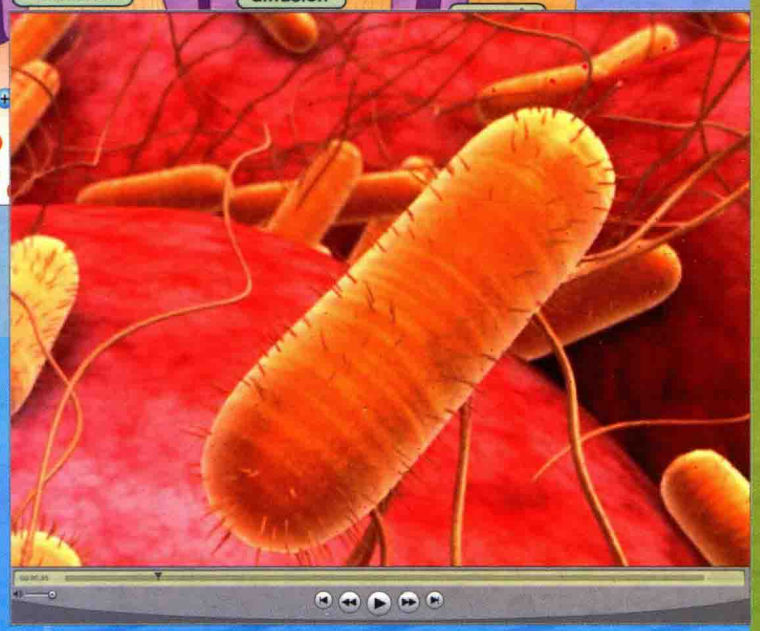

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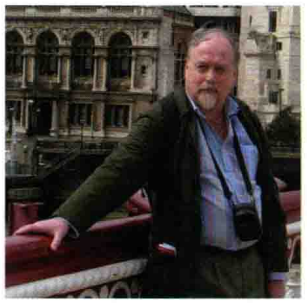
About the Authors

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 a three-year postdoctoral in the Department of Microbiology, Indiana University, Mike moved to Southern Illinois University–Carbondale, where he has been a professor of microbiology for 32 years. He has coauthored *Biology of Microorganisms* since the fourth edition (1984) and teaches courses in introductory microbiology, bacterial diversity, and diagnostic and applied microbiology. 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 (ASM), 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 12 years he has studied the microbiology of permanently ice-covered lakes in the McMurdo Dry Valleys, Antarctica. In addition to his research papers, he has edited a major treatise on phototrophic bacteria and served for over a decade 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 nonscientific interests include forestry, reading, and caring for his dogs and horses. He lives beside a peaceful and quiet lake with his wife, Nancy, five shelter dogs (Gaino, Snuffy, Pepto, Peanut, and Merry), and four horses (Springer, Feivel, 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–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. He retired in 2009, but remains active in the department as a researcher and teacher. His research investigates structural changes in major histocompatibility proteins. He teaches an advanced course in immunology and presents immunology and host defense lectures to medical students. He also chairs the Institutional Animal Care and Use Committee at SIUC. He has been active in educational outreach programs for pre-university students and teachers. For his educational efforts, he won the 2007 SIUC Outstanding Teaching Award. He is also an avid golfer and cyclist. John lives in Carbondale with his wife Judy, a high school science teacher.

David A. Stahl received his B.S. degree in Microbiology from the University of Washington–Seattle, later completing graduate studies in microbial phylogeny and evolution with Carl Woese in the Department of Microbiology at the University of Illinois–Champaign-Urbana. Subsequent work as a postdoctoral fellow with Norman Pace, then at the National Jewish Hospital in Colorado, focused on 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–Champaign-Urbana, holding 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 his alma mater, the University of Washington–Seattle, as a 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 Procter & Gamble Award in Applied and Environmental Microbiology from the ASM; he is also an elected Fellow of the American Academy of Microbiology. His main research interests are the biogeochemistry of nitrogen and sulfur compounds and the microbial communities that sustain these nutrient cycles. His laboratory was first to culture ammonia-oxidizing *Archaea*, a group now believed to be the main mediators of this key process in the nitrogen cycle. He has taught several courses in environmental microbiology, is one of the co-founding editors of the journal *Environmental Microbiology,* and has served on many advisory committees. Outside teaching and 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, Washington.



David P. Clark grew up in Croydon, a London suburb. He won a scholarship to Christ's College, Cambridge, where he received his B.A. degree in Natural Sciences in 1973. In 1977 he received his Ph.D. from Bristol University, Department of Bacteriology, for work on the effect of cell envelope composition on the entry of antibiotics into *Escherichia coli*. He then left England on a postdoctoral studying the genetics of lipid metabolism in the laboratory of John Cronan at Yale University. A year later he moved with the same laboratory to the University of Illinois at Urbana-Champaign. David joined the Department of Microbiology at Southern Illinois University–Carbondale in 1981. His research has focused on the growth of bacteria by fermentation under anaerobic conditions. He has published numerous research papers and graduated over 20 Masters and Doctoral students. In 1989 he won the SIUC College of Science Outstanding Researcher Award. In 1991 he was the Royal Society Guest Research Fellow at the Department of Molecular Biology and Biotechnology, Sheffield University, England. In addition to *Brock Biology of Microorganisms*, David is the author of four other science books: *Molecular Biology Made Simple and Fun,* now in its fourth edition; *Molecular Biology: Understanding the Genetic Revolution*; *Biotechnology: Applying the Genetic Revolution*; and *Germs, Genes, & Civilization: How Epidemics Shaped Who We Are Today.* David is unmarried and lives with two cats, Little George, who is orange and very nosey, and Mr. Ralph, who is mostly black and eats cardboard.

Dedications

Michael T. Madigan dedicates this book to the memory of his children who rest on Boot Hill: Andy, Marcy, Willie, Plum, Teal, and Sugar. Whether in good times or bad, they always greeted him with tails a waggin'.

John M. Martinko dedicates this book to his daughters Sarah, Helen, and Martha, and to his wife Judy. Thanks for all of your support!

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

David P. Clark dedicates this book to his father, Leslie, who set him the example of reading as many books as possible.

Preface

The authors and Benjamin Cummings Publishers proudly present the 13th edition of *Brock Biology of Microorganisms* (*BBOM* 13/e). This book is truly a milestone in the annals of microbiology textbooks. *Brock Biology of Microorganisms*, and its predecessor, *Biology of Microorganisms*, has introduced the field of microbiology to students for 41 years, more than any other textbook of microbiology. Nevertheless, although this book goes back over four decades, its two main objectives have remained firm since the first edition was published in 1970: (1) to present the principles of microbiology in a clear and engaging fashion, and (2) to provide the classroom tools necessary for delivering outstanding microbiology courses. The 13th edition of *BBOM* fulfills these objectives in new and exciting ways.

Veteran textbook authors Madigan, Martinko, and Clark welcome our new coauthor, Dave Stahl, to this edition of *BBOM*. Dave is one of the world's foremost experts in microbial ecology and has masterfully crafted an exciting new view of the ecology material in *BBOM*, including a new chapter devoted entirely to microbial symbioses, a first for any textbook of microbiology. Users will find that the themes of ecology and evolution that have permeated this book since its inception reach new heights in the 13th edition. These fundamental themes also underlie the remaining content of the book—the basic principles of microbiology, the molecular biology and genetics that support microbiology today, the huge diversity of metabolisms and organisms, and the medical and immunological facets of microbiology. It is our belief that outstanding content coupled with outstanding presentation have come together to make *BBOM* 13/e the most comprehensive and effective textbook of microbiology available today.

What's New in the 13th Edition?

In terms of content and pedagogy, instructors who have used *BBOM* previously will find the 13th edition to be the same old friend they remember; that is, a book loaded with accurate, up-to-the-minute content that is impeccably organized and visually enticing. The 36 chapters in *BBOM* 13/e are organized into modules by numbered head, which allows instructors to fine-tune course content to the needs of their students. In addition, study aids and review tools are an integral part of the text. Our new MiniQuiz feature, which debuts in the 13th edition, is designed to quiz students' comprehension as they work their way through each chapter. Also new to this edition is the end-of-chapter review tool called "Big Ideas." These capsule summaries pull together the key concepts from each numbered section in a wrap-up style that is certain to be a big hit with students, especially the night before examinations! Our end-of-chapter key terms list, two detailed appendices, a comprehensive glossary, and a thorough index complete the hard copy learning package. Many additional learning resources are available online (see below).

In terms of presentation, *BBOM* 13/e will easily draw in and engage the reader. The book has been designed in a beautiful yet simple fashion that gives the art and pedagogical elements the breathing room they need to be effective and the authors the freedom to present concepts in a more visually appealing way. Supporting the narrative are spectacular illustrations, with every piece of art rendered in a refreshing new style. Moreover, the art complements, and in many cases integrates, the hundreds of photos in *BBOM*, many of which are new to the 13th edition. And, as users of *BBOM* have come to expect, our distinctive illustrations remain the most accurate and consistent of those in any microbiology textbook today.

The authors are keenly aware that it is easy to keep piling on new material and fattening up a textbook. In response to this trend, *BBOM* 13/e went on a diet. With careful attention to content and presentation, *BBOM* 13/e is actually a shorter book than *BBOM* 12/e. The authors have carefully considered every topic to ensure that content at any point in the book is a reflection of both what the student already knows and what the student needs to know in a world where microbiology has become the most exciting and relevant of the biological sciences. The result is a more streamlined and exciting treatment of microbiology that both students and instructors will appreciate.

Revision Highlights:

Chapter 1

- Find new coverage on the evolution and major habitats of microorganisms—Earth's most pervasive and extensive biomass.
- A more visually compelling presentation of the impacts of microorganisms on humans better emphasizes the importance of microorganisms for the maintenance of all life on Earth.

Chapter 2

- New coverage of cell biology and the nature of the chromosome in prokaryotic and eukaryotic cells is complemented by a visually engaging overview of the microbial world.

Chapter 3

- The cell chemistry chapter that previously held this position is now available online (www.microbiologyplace.com). The new Chapter 3 explores cell structure and function with strong new visuals to carry the text and new coverage of the lipids and cell walls of *Bacteria* and *Archaea*.

Chapter 4

- Find updated coverage of catabolic principles along with an overview of essential anabolic reactions.
- Newly rendered and more instructive art makes mastering key metabolic pathways and bioenergetic principles a more visual experience.

Chapter 5

- Updated coverage of the events in cell division and their relation to medical microbiology connects basic science to applications.
- Newly rendered art throughout makes the important concepts of cell division and population growth more vivid, engaging, and interactive.

Chapter 6

- The concise primer on molecular biology that every student needs to know is updated and now includes an overview of the structures of nucleic acids and proteins and the nature of chromosomes and plasmids.

Chapter 7

- Find new coverage of the latest discoveries in the molecular biology of *Archaea* and comparisons with related molecular processes in *Bacteria*.
- A new section highlights the emerging area of regulation by microRNA in eukaryotes.

Chapter 8

- Review 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.
- Enjoy the new Microbial Sidebar featuring CRISPR, the newly discovered form of RNA-based regulation used by *Bacteria* and *Archaea* to ward off viral attack.

Chapter 9

- Major updates of the principles of virology are complemented with an overview of viral diversity.
- New art reinforces the relevance and importance of viruses as agents of genetic exchange.

Chapter 10

- The fundamental principles of microbial genetics are updated and supplemented with new coverage that compares and contrasts bacterial and archaeal genetics.

Chapter 11

- Find "one-stop shopping" for coverage of molecular biological methods, including cloning and genetic manipulations, as a prelude to the genomics discussion in the next chapter.
- Enjoy the colorful new Microbial Sidebar on new fluorescent labeling methods that can differentiate even very closely related bacteria.

Chapter 12

- Extensive updates on microbial genomics and transcriptomics will be found along with new coverage of the emerging related areas of metabolomics and interactomics.

Chapter 13

- The two chapters covering metabolic diversity have been revised and moved up to Chapters 13 and 14 to precede rather than follow coverage of microbial diversity, better linking these two important and often related areas.
- This chapter is loaded with reworked art and text that highlight the unity and diversity of the bioenergetics underlying phototrophic and chemolithotrophic metabolisms.

Chapter 14

- Restyled and impeccably consistent art showcases the comparative biochemistry of the aerobic and anaerobic catabolism of carbon compounds.

Chapter 15

- This retooled chapter combines the essentials of industrial microbiology and biotechnology, including the production of biofuels and emerging green microbial technologies.

Chapter 16

- Find new coverage of the origin of life and how the evolutionary process works in microorganisms.
- Microbial phylogenies from small subunit ribosomal RNA gene analyses are compared with those from multiple-gene and full genomic analyses.

Chapters 17–19

- Coverage of the diversity of *Bacteria* and *Archaea* better emphasizes phylogeny with increased focus on phyla of particular importance to plants and animals and to the health of our planet.
- Spectacular photomicrographs and electron micrographs carry the reader through prokaryotic diversity.

Chapter 20

- A heavily revised treatment of the diversity of microbial eukaryotes is supported by many stunning new color photos and photomicrographs.
- Find an increased emphasis on the phylogenetic relationships of eukaryotes and the "bacterial nature" of eukaryotic organelles.

Chapter 21

- Viruses, the most genetically diverse of all microorganisms, come into sharper focus with major updates on their diversity.
- A new section describes viruses in nature and their abundance in aquatic habitats.

Chapter 22

- This chapter features a major new treatment of the latest molecular techniques used in microbial ecology, including CARD-FISH, ARISA, biosensors, NanoSIMS, flow cytometry, and multiple displacement DNA amplification.
- Find exciting new coverage of methods for functional analyses of single cells, including single-cell genomics and single-cell stable isotope analysis, and expanded coverage of methods for analyses of microbial communities, including metagenomics, metatranscriptomics, and metaproteomics.

Chapter 23

- A comparison of the major habitats of *Bacteria* and *Archaea* is supported by spectacular new photos and by art that summarizes the phylogenetic diversity and functional significance of prokaryotes in each habitat.
- Find broad new coverage of the microbial ecology of microbial mat communities and prokaryotes that inhabit the deep subsurface.

Chapter 24

- Revised coverage of the classical nutrient cycles is bolstered by new art, while new coverage highlights the calcium and silica cycles and how these affect CO_2 sequestration and global climate.
- Improved integration of biodegradation and bioremediation shows how natural microbial processes can be exploited for the benefit of humankind.

Chapter 25

- This new chapter focuses entirely on microbial symbioses, including bacterial–bacterial symbioses and symbioses between bacteria and their plant, mammal, or invertebrate hosts. Find coverage here of all of the established as well as more recently discovered symbioses, including the human gut and how its microbiome may control obesity, the rumen of animals important to agriculture, the hindgut of termites, the light organ of the squid, the symbioses between hydrothermal vent animals and chemolithotrophic bacteria, the essential bacterial symbioses of insects, medicinal leeches, reef-building corals, and more, all supported by spectacular new color photos and art.
- Learn how insects have shaped the genomes of their bacterial endosymbionts.
- Marvel at the new Microbial Sidebar that tells the intriguing story of the attine ants and their fungal gardens.

Chapter 26

- Key updates will be found on microbial drug resistance and are supported by new art that reveals the frightening reality that several human pathogens are resistant to all known antimicrobial drugs.

Chapter 27

- Extensively reworked sections on the normal microbial flora of humans include new coverage of the human microbiome and a molecular snapshot of the skin microflora.
- Find revised coverage of the principles of virulence and pathogenicity that connect infection and disease.

Chapter 28

- Here we present the perfect overview of immunology for instructors who wish to cover only the fundamental concepts and how the immune system resists the onslaught of infectious disease.
- Find late-breaking practical information on the immune response, including vaccines and immune allergies.

Chapter 29

- Built on the shoulders of the previous chapter, here is a more detailed probe of the mechanisms of immunity with emphasis on the molecular and cellular interactions that control innate and adaptive immunity.

Chapter 30

- This short chapter presents an exclusively molecular picture of immunology, including receptor–ligand interactions (the "triggers" of the immune response), along with genetics of the key proteins that drive adaptive immunity.

Chapter 31

- Find revised and expanded coverage of molecular analyses in clinical microbiology, including new enzyme immunoassays, reverse transcriptase PCR, and real-time PCR.

Chapter 32

- Review major updates of the principles of disease tracking, using 2009 pandemic H1N1 influenza as a model for how newly emerging infectious diseases are tracked.
- Find updated coverage throughout, especially of the HIV/AIDS pandemic.

Chapter 33

- Read all about the origins and history of pandemic H1N1 influenza and how the H1N1 virus is related to strains of influenza that already existed in animal populations.
- Hot new coverage of immunization strategies for HIV/AIDS.

Chapter 34

- Follow the emergence, rapid dispersal, and eventual entrenchment of West Nile virus as an endemic disease in North America.
- Expanded coverage of malaria—the deadliest human disease of all time—includes the promise of new antiparasitic drugs and disease prevention methods.

Chapter 35

- Find updates of water microbiology, including new rapid methods for detecting specific indicator organisms.

Chapter 36

- Explore new methods of food processing, including aseptic and high-pressure methods that can dramatically extend the shelf-life and safety of perishable foods and drinks.

Cutting Edge Coverage Includes the Most Current Presentation of Microbial Ecology

The 13th edition enhances the themes of ecology and evolution throughout, and is the only book on the market to include specialized coverage of archael and eukaryotic molecular biology. The book represents the most current research in the field, with special attention paid to the microbial ecology chapters:

Chapter 22, Methods in Microbial Ecology, is heavily updated to present the latest molecular techniques used in microbial ecology, including CARD-FISH, ARISA, biosensors, NanoSIMS, flow cytometry, and multiple displacement DNA amplification. It also includes exciting new coverage of methods for functional analyses of single cells, including single-cell genomics and single-cell stable isotope analysis, and expanded coverage of methods for analyses of microbial communities, including metagenomics, metatranscriptomics, and metaproteomics.

Chapter 23, Major Microbial Habitats and Diversity, compares the major habitats of *Bacteria* and *Archaea* and is supported by spectacular new photos and art that summarize the phylogenetic diversity and functional significance of prokaryotes in each habitat.

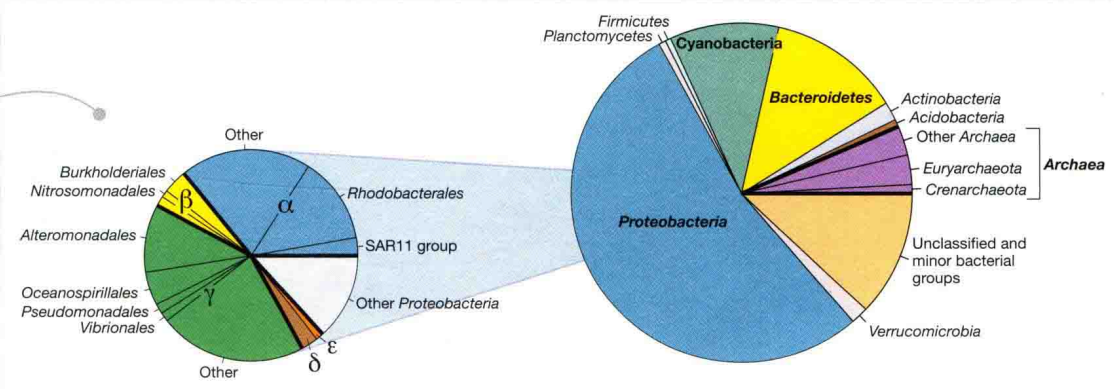


Figure 23.24 **Ocean prokaryotic diversity.** The results are pooled analyses of 25,975 sequences from several studies of the 16S rRNA gene content of pelagic ocean waters. Many of these groups are covered in Chapters 17 and 18 (*Bacteria*) or 19 (*Archaea*). For *Proteobacteria*, major subgroups are indicated. Note the high proportion of cyanobacterial and *Gammaproteobacteria* sequences. Data assembled and analyzed by Nicolas Pinel.

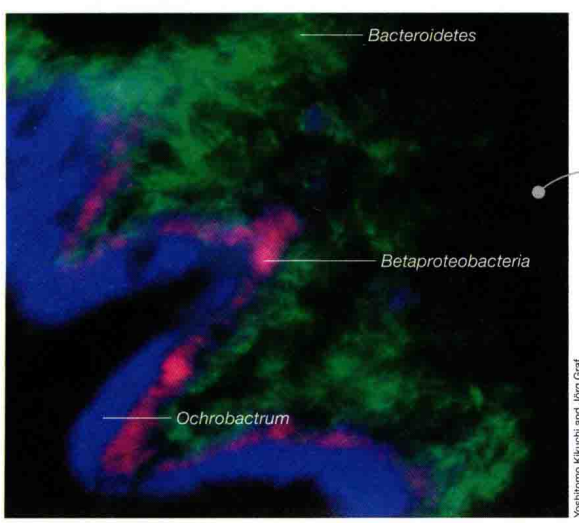


Figure 25.40 **Micrograph of a FISH-stained microbial community in the bladder of *Hirudo verbana*.** A probe (red) targeted at the 16S rRNA of *Betaproteobacteria* and a probe (green) targeted at the 16S rRNA of *Bacteroidetes* reveal distinct layers of different bacteria in the lumen of the bladder. Staining with DAPI (blue), which binds to DNA, reveals the intracellular alphaproteobacterium *Ochrobactrum* and host nuclei.

Chapter 24, Nutrient Cycles, Biodegradation, and Bioremediation. Exciting updates of all the nutrient cycles that form the heart of environmental microbiology and microbial ecology.

Chapter 25, Microbial Symbioses, is a completely new chapter focused entirely on microbial symbioses, including bacterial–bacterial symbioses and symbioses between bacteria and their plant, mammal, or invertebrate hosts. Find coverage here of all the established as well as more recently discovered symbioses—including the human gut and how its microbiome may control obesity, the rumen of animals important to agriculture, the hindgut of termites, the light organ of the squid, the symbioses between hydrothermal vent animals and chemolithotrophic bacteria, and the essential bacterial symbioses of insects, medicinal leeches, reef-building corals, and more.

For a detailed list of chapter-by-chapter updates, see page 5 of the Preface.

Thoroughly Updated and Revised Art

The art has been revised and updated throughout the book to give students a clear view into the microbial world. Color and style conventions are used consistently to make the art accessible and easy to understand.

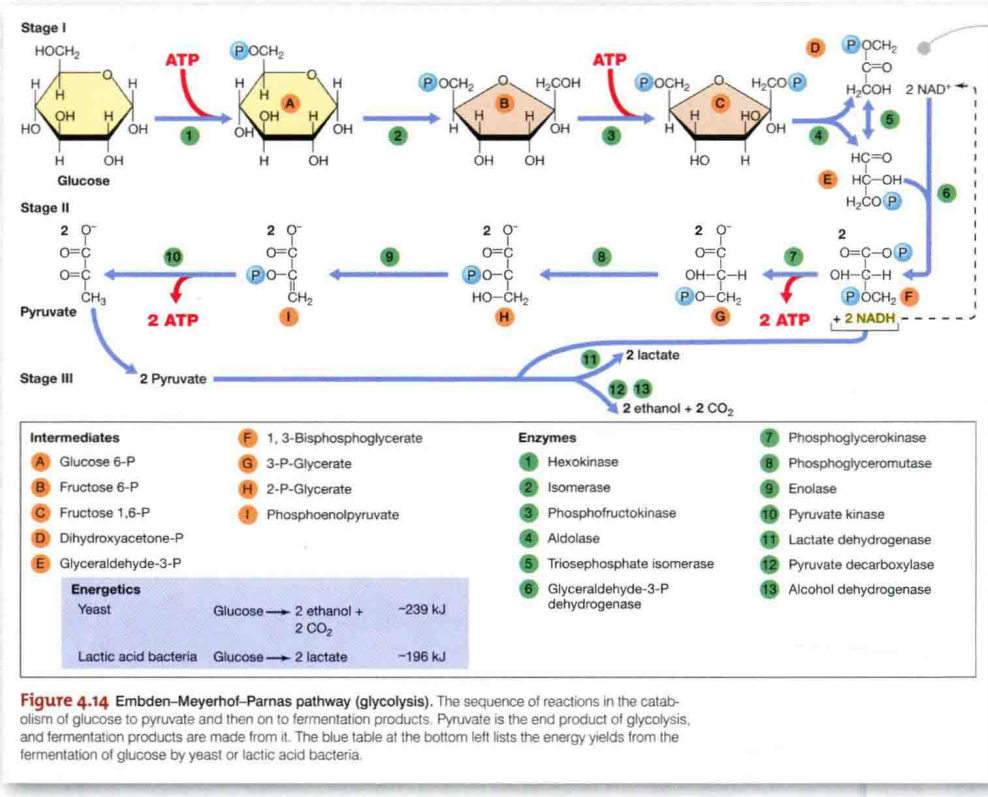


Figure 4.14 Embden–Meyerhof–Parnas pathway (glycolysis). The sequence of reactions in the catabolism of glucose to pyruvate and then on to fermentation products. Pyruvate is the end product of glycolysis, and fermentation products are made from it. The blue table at the bottom left lists the energy yields from the fermentation of glucose by yeast or lactic acid bacteria.

Carefully redesigned new art clearly guides students through challenging concepts. The style for metabolic figures and other pathway processes has been simplified, and color-coded steps and chemical structures increase student comprehension.

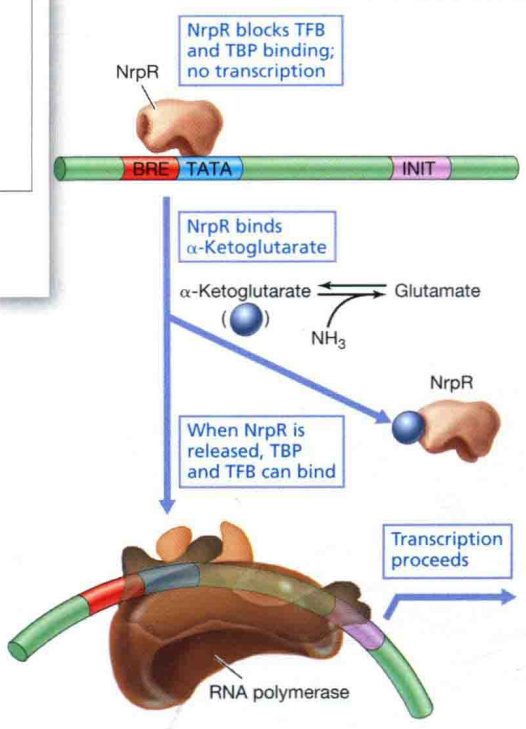


Figure 8.15 Repression of genes for nitrogen metabolism in *Archaea*. The NrpR protein of *Methanococcus maripaludis* acts as a repressor. It blocks the binding of the TFB and TBP proteins, which are required for promoter recognition, to the BRE site and TATA box, respectively. If there is a shortage of ammonia, α-ketoglutarate is not converted to glutamate. The α-ketoglutarate accumulates and binds to NrpR, releasing it from the DNA. Now TBP and TFB can bind. This in turn allows RNA polymerase to bind and transcribe the operon.

Dimensionality has been added to some figures, lending more realism and vivacity to the presentation. Figures in which nucleic acids or cells are depicted are now more dimensional to clearly identify key genes and cell structures.

Illustrations and photos are often paired to give an idealized view next to a realistic view and to reinforce the connection between theory and practice.

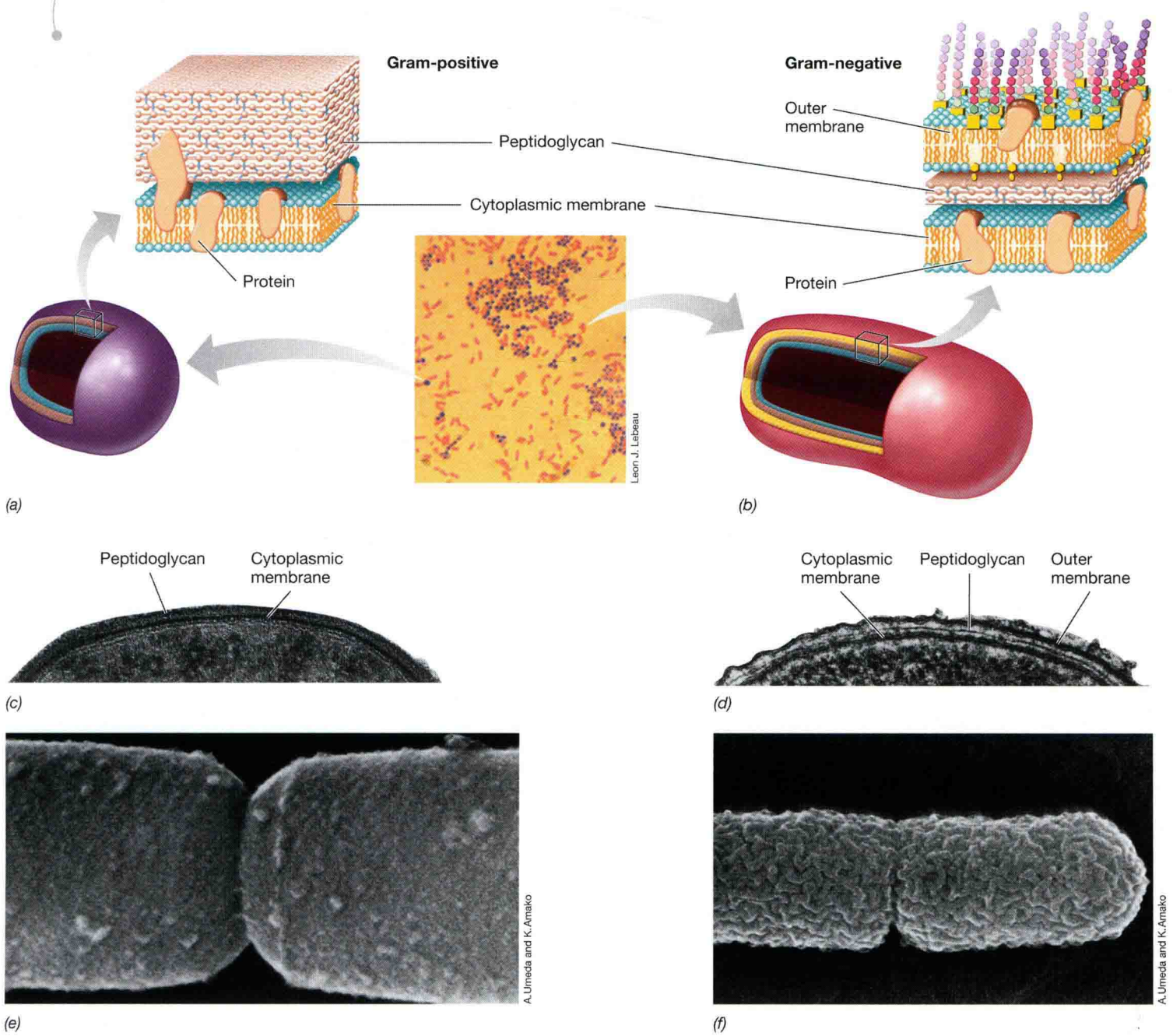


Figure 3.15 **Cell walls of *Bacteria*.** *(a, b)* Schematic diagrams of gram-positive and gram-negative cell walls. The Gram stain photo in the center shows cells of *Staphylococcus aureus* (purple, gram-positive) and *Escherichia coli* (pink, gram-negative). *(c, d)* Transmission electron micrographs (TEMs) showing the cell wall of a gram-positive bacterium and a gram-negative bacterium. *(e, f)* Scanning electron micrographs of gram-positive and gram-negative bacteria, respectively. Note differences in surface texture. Each cell in the TEMs is about 1 μm wide.

Conceptual Framework Helps Students Focus on the Key Concepts

The first twelve chapters cover the principles of microbiology. Basic principles are presented early on and then used as the foundation to tackle the material in greater detail later.

Brief Contents

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New chapter on symbiosis ties together the core concepts of the book—health, diversity, and the human ecosystem.

This newly revised chapter is the perfect overview for instructors who wish to cover immunology at a generalized level including the fundamental concepts of how the immune system resists the onslaught of infectious disease. Instructors who like to go into more detail can build on the core principles taught in Chapter 28 by covering Immune Mechanisms (Ch. 29) and Molecular Immunology (Ch. 30).

Information on metabolic diversity precedes the coverage of microbial diversity, better linking these important and often related areas.