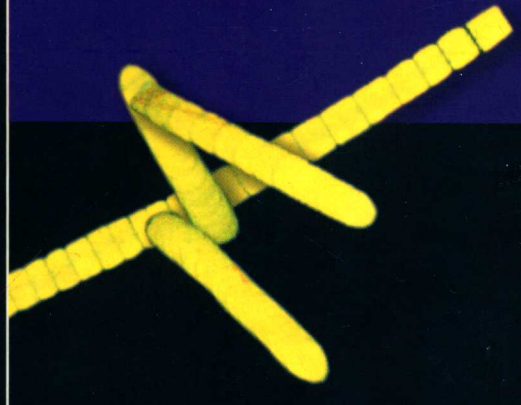
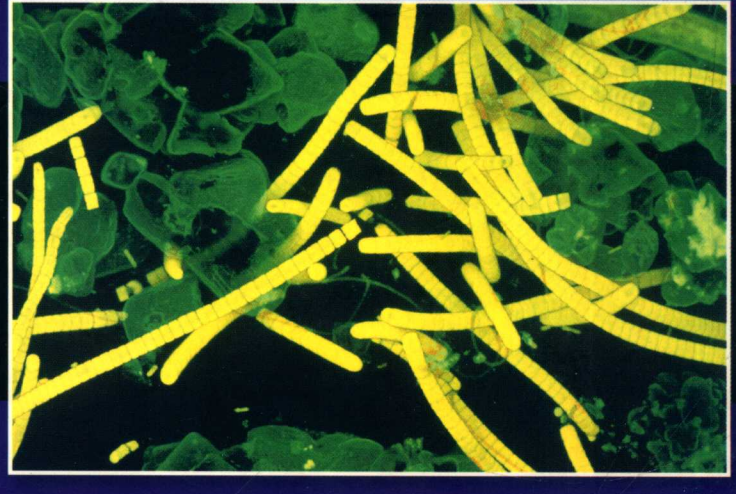
INTERNATIONAL EDITION

ELEVENTH EDITION

BROCK BIOLOGY OF MICROORGANISMS

MICHAEL T. MADIGAN





JOHN M. MARTINKO

BROCK

Eleventh Edition

BIOLOGY OF MICROORGANISMS

Michael T. Madigan

John M. Martinko

Southern Illinois University Carbondale

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Pearson Prentice Hall
Pearson Education, Inc.
Upper Saddle River, NJ 07458

First through seventh editions titled *Biology of Microorganisms*

Editions of Biology of Microorganisms
First Edition, 1970, Thomas D. Brock
Second Edition, 1974, Thomas D. Brock
Third Edition, 1979, Thomas D. Brock
Fourth Edition, 1984, Thomas D. Brock, David W. Smith, and Michael T. Madigan
Fifth Edition, 1988, Thomas D. Brock and Michael T. Madigan
Sixth Edition, 1991, Thomas D. Brock and Michael T. Madigan
Seventh Edition, 1994, Thomas D. Brock, Michael T. Madigan, John M. Martinko, and Jack Parker
Eighth Edition, 1997, Michael T. Madigan, John M. Martinko, and Jack Parker
Ninth Edition, 2000, Michael T. Madigan, John M. Martinko, and Jack Parker
Tenth Edition, 2003, Michael T. Madigan, John M. Martinko, and Jack Parker
Eleventh Edition, 2006, Michael T. Madigan and John M. Martinko

Printed in the United States of America

10 9 8 7 6 5 4 3 2 1

ISBN 0-13-196893-9

Pearson Education LTD., *London*
Pearson Education Australia PTY, Limited, *Sydney*
Pearson Education Singapore, Pte. Ltd.
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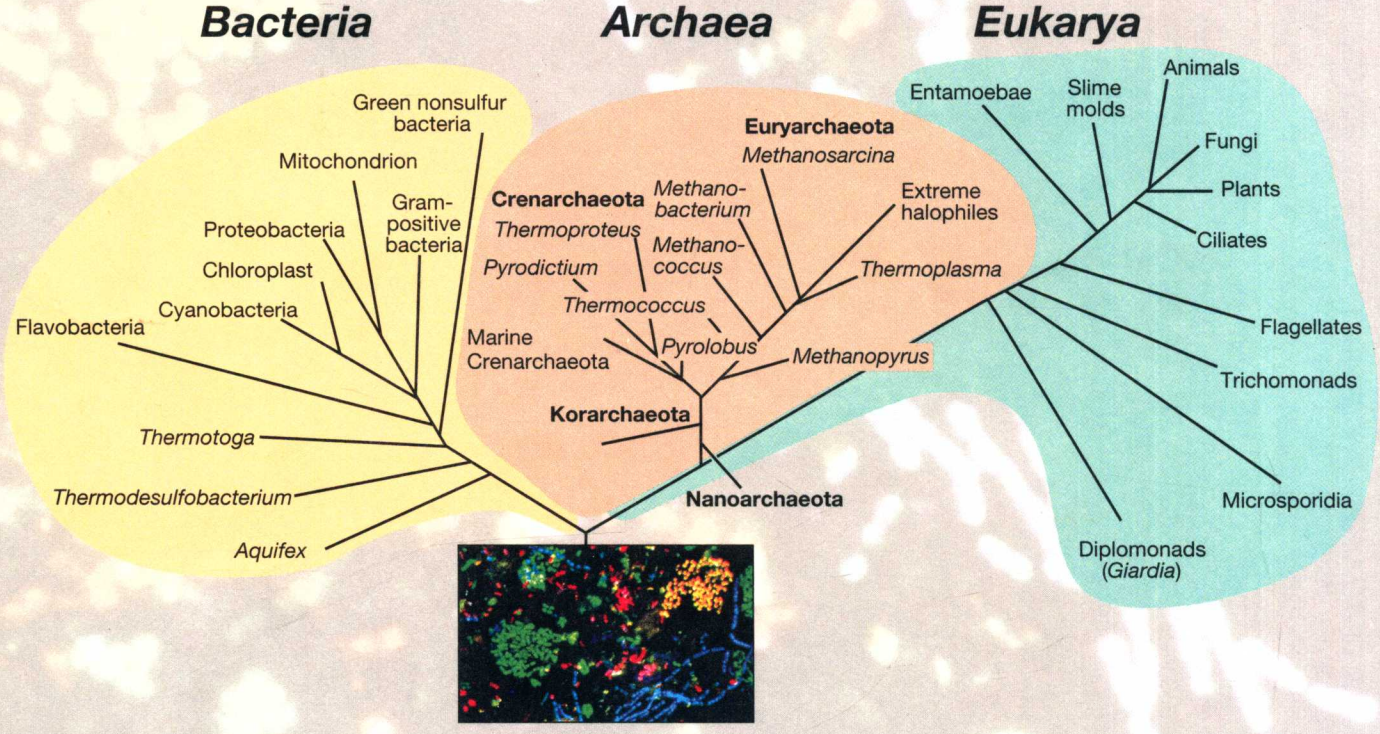
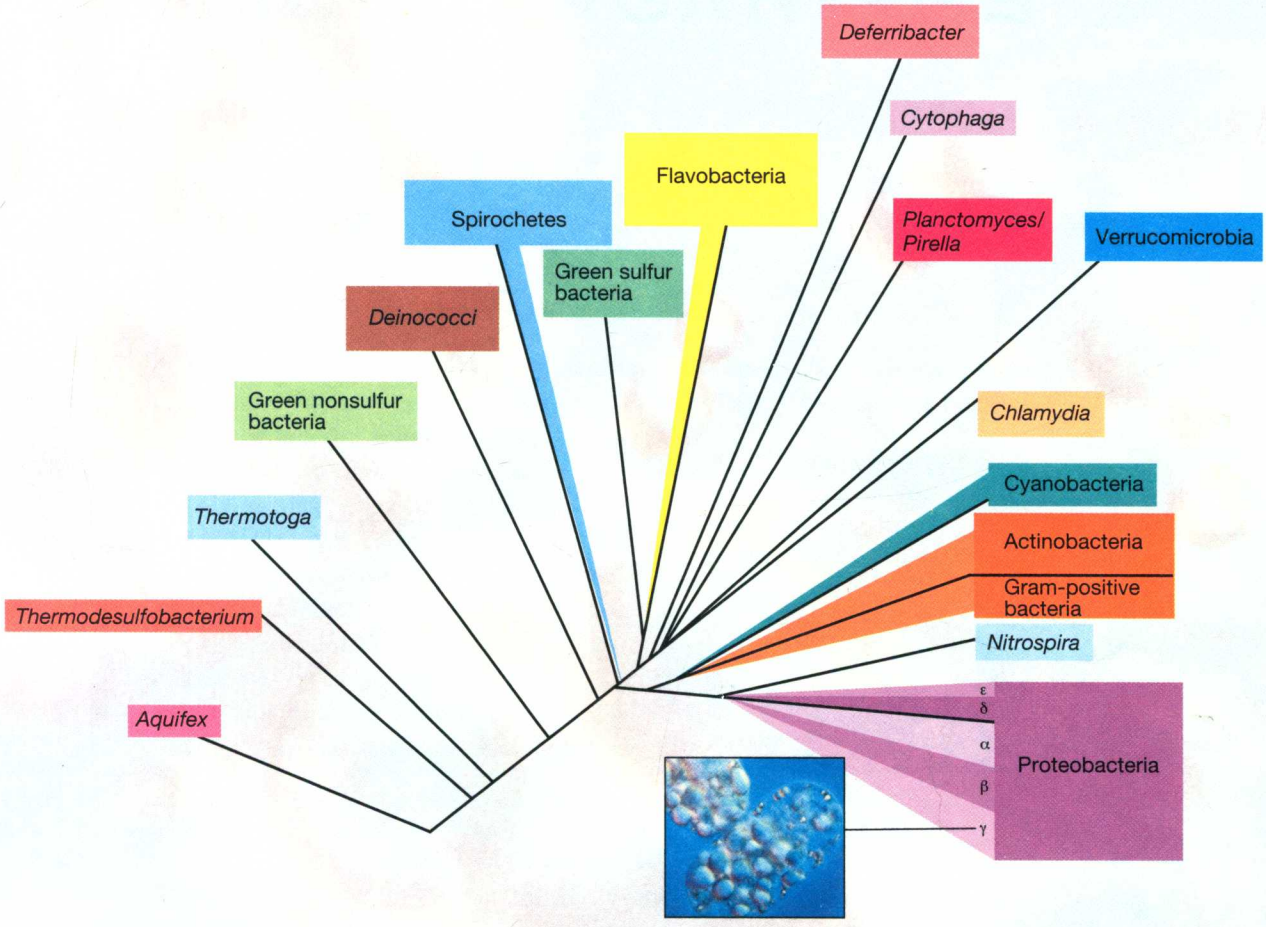
PHYLOGENY OF THE LIVING WORLD–OVERVIEW



UNIVERSAL PHYLOGENETIC TREE. This tree is derived from comparative sequencing of 16S or 18S ribosomal RNA. Note the three major domains of living organisms: the *Bacteria*, the *Archaea*, and the *Eukarya*. The evolutionary distance between two groups of organisms is proportional to the cumulative distance between the end of the branch and the node that joins the two groups. See Sections 11.5–11.9 for further information on ribosomal RNA-based phylogenies. The phylogenetic relationships depicted in this tree have been supported by several other genotypic and phenotypic relationships. *Data for the tree obtained from the Ribosomal Database project* **http://rdp.cme.msu.edu**

PHYLOGENY OF THE LIVING WORLD–*BACTERIA*



PHYLOGENETIC TREE OF *BACTERIA*. This tree is derived from 16S ribosomal RNA sequences. At least 17 major groups of *Bacteria* can be defined as indicated. See Sections 11.5–11.9 for further information on ribosomal RNA-based phylogenies. *Data for the tree obtained from the Ribosomal Database project* **http://rdp.cme.msu.edu**

BROCK

BIOLOGY OF MICROORGANISMS

MICHAEL T. MADIGAN dedicates this book to the two old friends pictured with him below: Willie (left) and Plum (right). For the past 11 years these wonderful animals have given me the comfort and companionship that only a dog lover could understand. Willie is, and always has been, the paragon of a sweet dog. Plum (deceased April 16, 2004), by contrast, was your basic junkyard dog. But in reality, she had a heart of gold and loved people, and our paths never crossed that she wasn't thrilled to see me. Rest in peace amigo.

JOHN M. MARTINKO dedicates this book to his students, past and present. The best students continually present problems from new perspectives, inspiring me to not only teach, but to expand my knowledge and enhance my understanding. To all who I have had the pleasure to teach, thank you for teaching me!

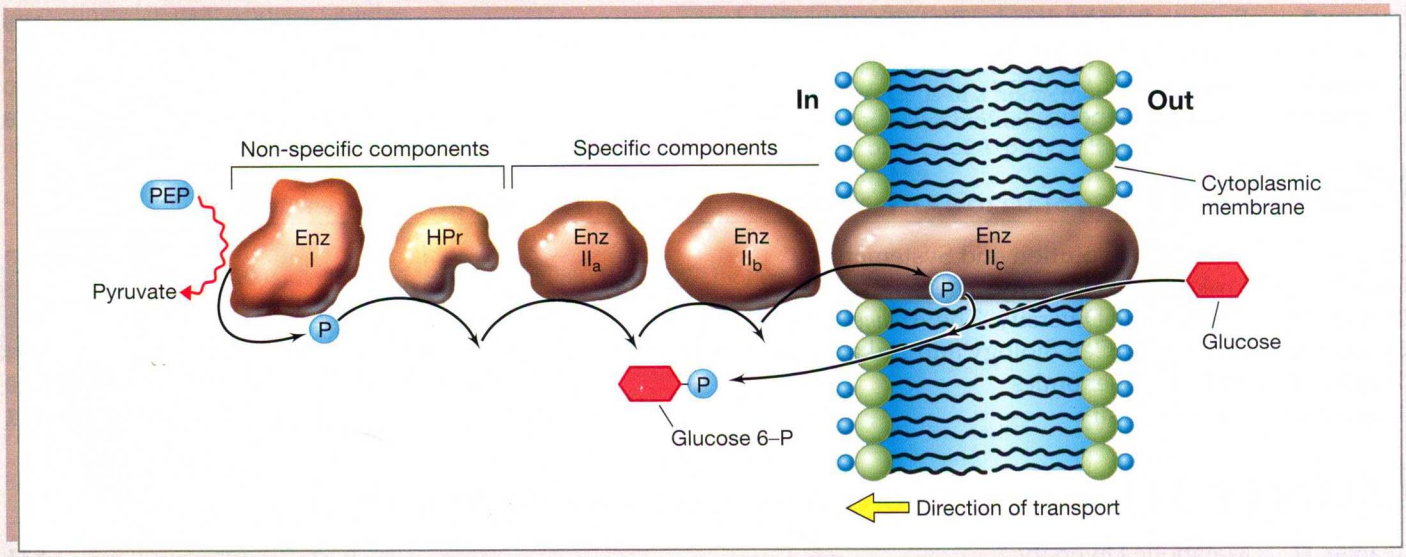
ABOUT THE AUTHORS

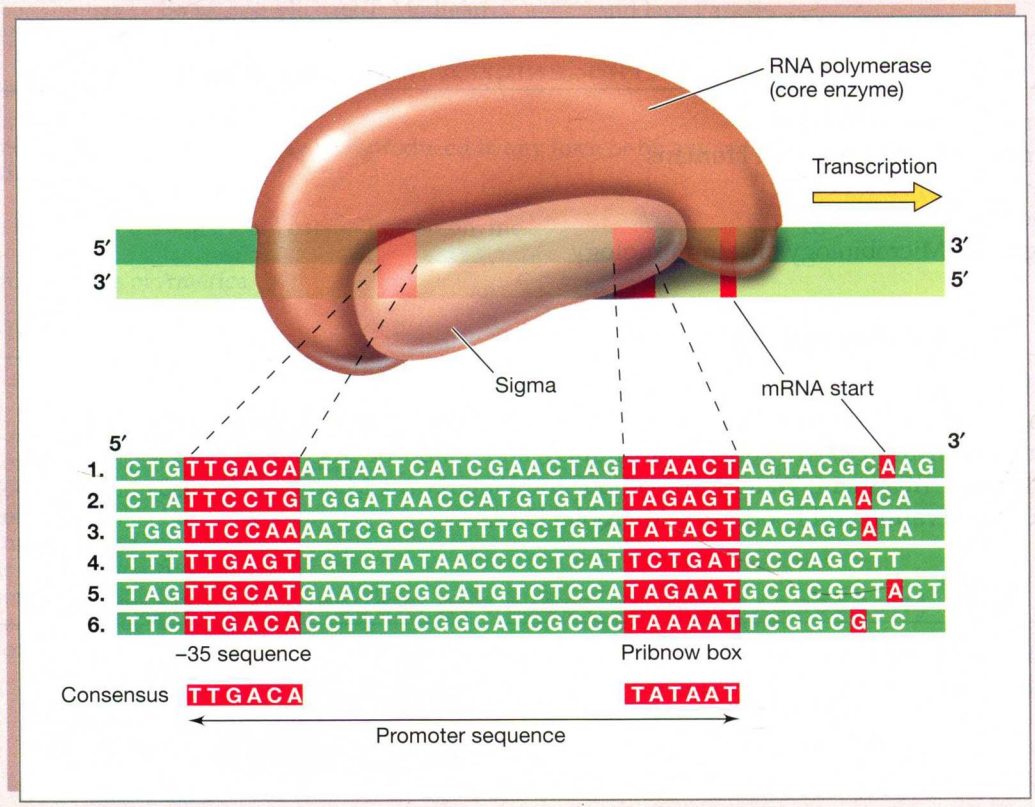
MICHAEL T. MADIGAN received a bachelor's degree in biology and education from Wisconsin State University at Stevens Point in 1971 and M.S. and Ph.D. degrees in 1974 and 1976, respectively, from the University of Wisconsin, Madison, Department of Bacteriology. His graduate work involved the study of hot spring phototrophic bacteria under the direction of Thomas D. Brock. Following three years of postdoctoral training in the Department of Microbiology, Indiana University, where he worked on phototrophic bacteria with Howard Gest, he moved to Southern Illinois University Carbondale, where he is a Professor of Microbiology. He has been a coauthor of *Biology of Microorganisms* since the fourth edition (1984) and teaches courses in introductory microbiology, bacterial diversity, and diagnostic and applied microbiology. In 1988 he was selected as the outstanding teacher in the College of Science, and in 1993 its outstanding researcher. In 2001 he received the university's Outstanding Scholar Award. In 2003 he received the Carski Award for Distinguished Teaching of Undergraduates from the American Society of Microbiology. His research has dealt almost exclusively with anoxygenic phototrophic bacteria, especially those species that inhabit extreme environments. He has published over 100 research papers, has coedited a major treatise on phototrophic bacteria, and has served as editor and chief editor of the journal *Archives of Microbiology*. His nonscientific interests include reading, hiking, tree planting, and caring for his dogs and horses. He lives beside a quiet lake about five miles from the SIU campus with his wife, Nancy, two dogs, Willie and Pupagano, and Springer and Feivel (horses).

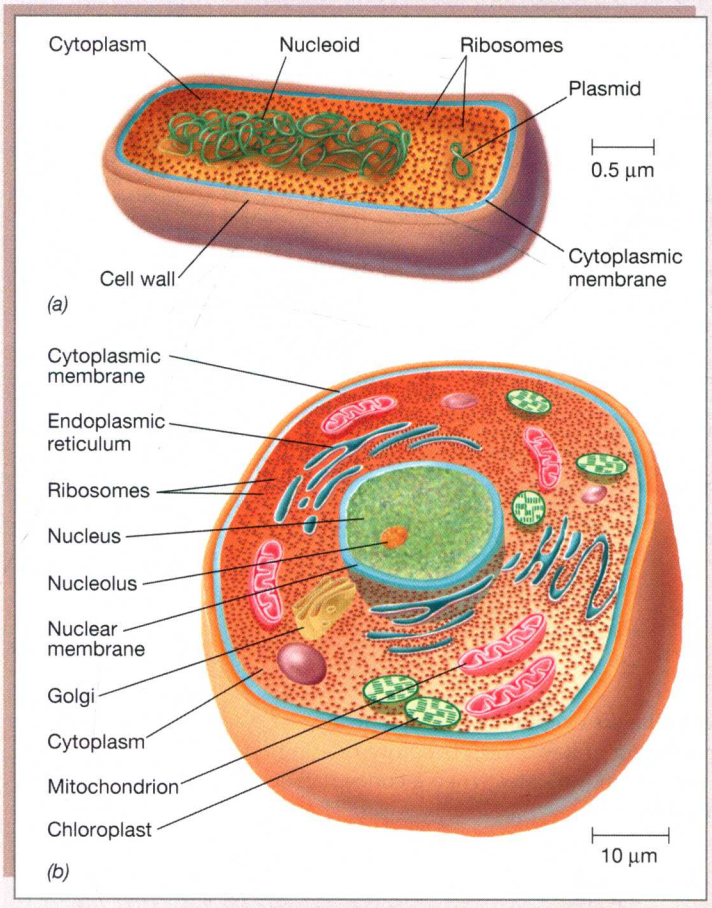
JOHN M. MARTINKO received his B.S. in Biology from The Cleveland State University. As an undergraduate student he participated in a cooperative education program, gaining experience in several microbiology and immunology laboratories. He then worked for two years at Case Western Reserve University as a laboratory manager, conducting research on the structure, serology and epidemiology of Streptococcus pyogenes. He did his graduate work at the State University of New York at Buffalo, investigating antibody specificity and antibody idiotypes for his M.A. and Ph.D. in Microbiology. 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 is an Associate Professor and Chair. His research interests include the effects of growth hormone in the immune response, the development of immunodiagnostic tests for soybean brown stem rot disease, and the investigation of structural mutations that alter function in peptide-major histocompatibility protein complexes. His teaching interests include undergraduate and graduate courses in immunology. He also teaches immunology, host defense, and infectious disease topics in a general microbiology course. In 2004, he was selected the outstanding teacher in the College of Science. He is also an avid golfer and cyclist. He lives in Carbondale with his wife, Judy, a high school science teacher.

ELEVENTH EDITION OVERVIEW

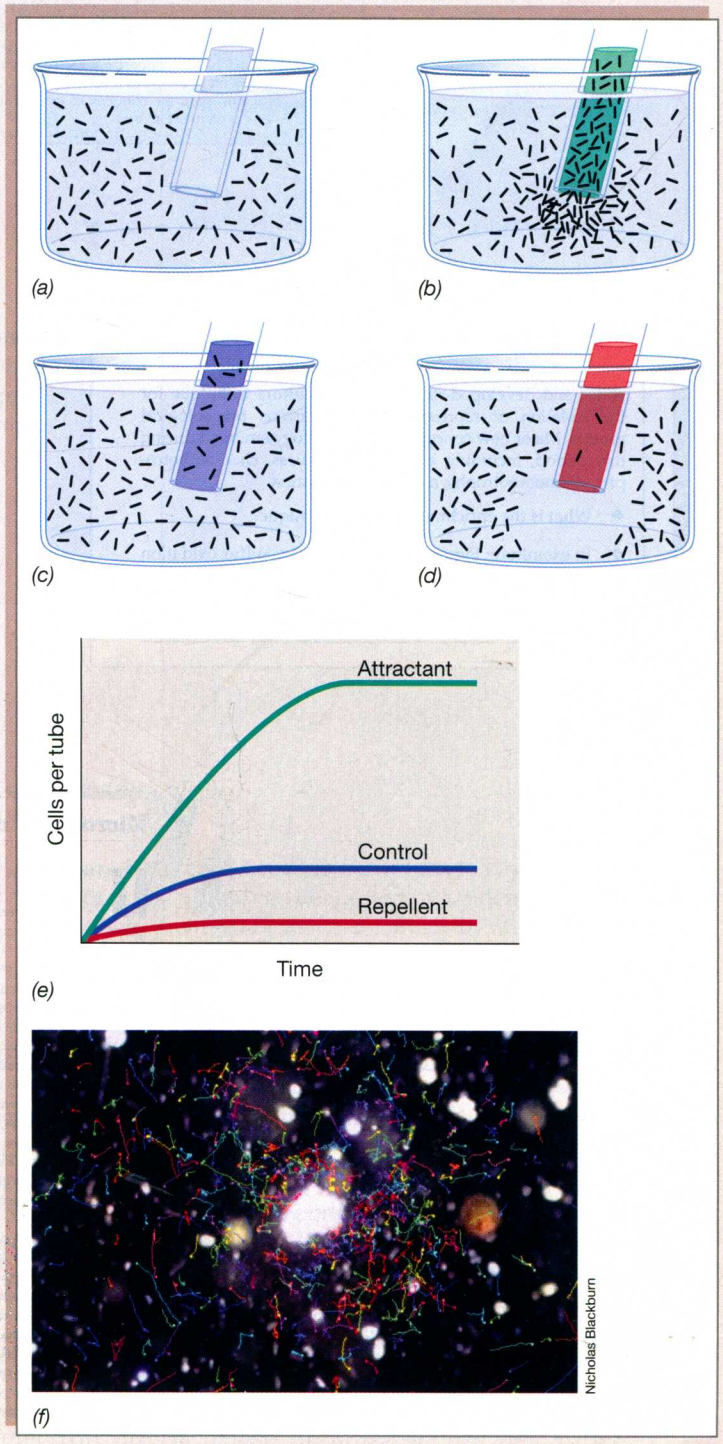
Each edition creates an opportunity to clarify concepts through the graphics, and *BBOM* has the most exceptional **Illustration Program** in microbiology. Students rely on graphics more each year, and *BBOM* remains dedicated to providing figures, photos and tables that are not only visually engaging, but focused on helping students to better understand the material. ▼







▲ Geared toward today's visual learners, hundreds of graphics in the 11th edition have been completely redesigned and improved upon to provide greater depth and realism.



Wherever possible, techniques and processes include photomicrographs that link abstract representations to biological reality. ▶

COMPREHENSION

The **Working Glossary** is the students' guide to the language of microbiology. By beginning each chapter with the glossary, students can more easily master terminology and increase their understanding of key concepts. ▶

WORKING GLOSSARY

Bacteriophage a virus that infects prokaryotic cells
Early protein a protein synthesized soon after virus infection
Late protein a protein synthesized toward the end of virus infection
Lysogen a bacterium containing a prophage
Lysogenic pathway a series of steps that, after virus infection, lead to a state (lysogeny) where the viral genome is replicated as a prophage along with that of the host
Lytic pathway a series of steps after virus infection that leads to virus replication and the destruction (lysis) of the host cell
Minus (negative)-strand virus a virus with an RNA genome in which the RNA strand has the opposite sense of (is complementary to) the mRNA of the virus
Nucleocapsid the complex of nucleic acid and proteins of a virus
Oncogene a gene whose expression causes formation of a tumor
Plaque a zone of lysis or cell inhibition caused by virus infection of a lawn of sensitive cells
Plus (positive)-strand virus a virus with an RNA or DNA genome in which the genome has the same complementarity as the mRNA of the virus
Prion an infectious protein whose extracellular form contains no nucleic acid
Provirus (prophage) the genome of a temperate virus when it is replicating with, and usually integrated into, the host chromosome
Retrovirus a virus whose RNA genome has a DNA intermediate as part of its replication cycle
Reverse transcription the process of copying information found in RNA into DNA by the enzyme reverse transcriptase
Temperate virus a virus whose genome is able to replicate along with that of its host and not cause cell death in a state called lysogeny
Transformation in eukaryotes, a process by which a normal cell becomes a cancer cell (but see alternative usage in Chapter 10)
Virion the complete virus particle; the nucleic acid surrounded by a protein coat and in some cases other material
Virulent virus a virus that lyses or kills the host cell after infection; a nontemperate virus
Virus a genetic element containing either RNA or DNA that replicates in cells but is characterized by having an extracellular state
Viroid small, circular, single-stranded RNA that causes various plant diseases

1.7 Concept Check

Beijerinck and Winogradsky studied bacteria in soil and water and developed the enrichment culture technique for the isolation of representatives of various physiological groups. Major new concepts in microbiology emerged during this period, including enrichment cultures, chemolithotrophy, chemoautotrophy, and nitrogen fixation.

- What is the enrichment culture technique?
- In examining Figure 1.16, describe why sulfur oxidation and nitrification are considered chemolithotrophic processes while nitrogen fixation is not. (*Hint:* Look at the reactions involving ATP in each case.)

◀ **Concept Checks** encourage students to stop and assess their understanding of key concepts before moving on. A new "stop sign" icon indicates when a concept check appears in the narrative.

Microbial Sidebar ◆ RNA Editing

In Chapters 7 and 14 we saw that certain genes have coding regions that are split by noncoding regions called *introns*. Typically, introns are removed after transcription to form a mature mRNA, a process called *splicing* (Section 14.8). Interestingly, there is a phenomenon found in the genomes of organelles that is almost the opposite of splicing: *RNA editing*.

RNA editing involves either the insertion or deletion of nucleotides *into the final mRNA* that were not present in the DNA transcribed. Editing can also involve the chemical *modification* of a base in the mRNA that changes it from one base to another. In either case, RNA editing can alter codons in such a way that one or more different amino acids are inserted in a polypeptide than those encoded by its gene.

In the mitochondria of trypanosomes and related protozoa (Section 14.10) some mitochondrial transcripts are edited such that large numbers (hundreds in some cases) of uridylates are added or, more rarely, deleted. An example of this type of RNA editing is shown in Figure 1●. RNA editing is precisely controlled by short sequences present in the mRNA that "guide" the enzymes involved in their specific edits. Obviously this process must be very precisely controlled. Inserting too many or too few bases would yield a frameshift product that would likely be nonfunctional.

The other type of RNA editing, the changing of one base into another, is common in the mitochondria and chloroplasts of higher plants. At specific sites in some mRNAs, a C will be converted to a U by oxidative deamination (the opposite modification is more rare). There are at least 25 sites of C to U conversion in the maize chloroplast. Although mostly found in organellar genomes, an example of the programmed conversion of a C to a U is also known for a mammalian nuclear gene. Depending on the location of the edit, a new codon may be formed, leading to formation of a protein sequence not predictable from the gene that encodes it.

RNA editing, although a curious phenomenon, was not a significant obstacle in analyzing *organellar* genomes. This is because the number of proteins they encode is small and the proteins highly conserved. By contrast, had RNA editing been a widespread phenomenon in *cells*, genomic annotations and the identification of orthologous genes in different organisms could have been an even more formidable challenge than it has been to date.

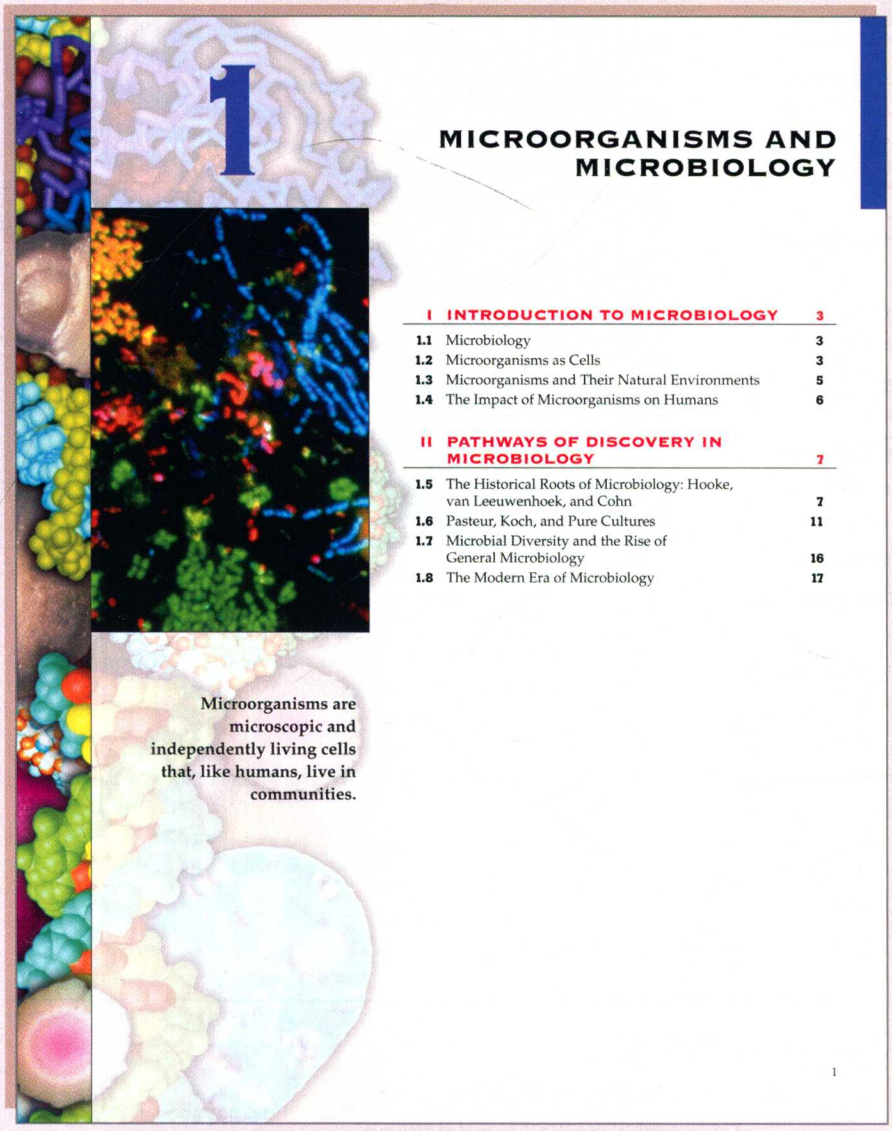
The function and origin of RNA editing is unknown. But some scientists have pointed out that this process may be yet another remnant, along with ribozymes (Section 14.8) and other catalytic RNAs, of the RNA World (Section 11.2). ■

Protein	...Leu Cys Phe Trp Phe Arg Phe Phe Cys...
mRNA	...uuG uGu UUU UGG uuu AGG uuu uuu uGu...
DNA	... G G TTT TCC AGG G ...
	... C C AAA AGG TCC C ...

***Figure 1* RNA editing**. *The upper part of the figure shows a portion of the amino acid sequence of subunit III of the enzyme cytochrome oxidase from the protozoan* Trypanosoma brucei *(Section 14.10). This protein is encoded by mitochondria. Beneath the amino acid sequence, the sequence of the messenger RNA (mRNA) for this region is shown. The bases in uppercase letters are those transcribed from the gene, which is shown below. The bases in the mRNA in lowercase have been inserted into the transcript by RNA editing. Although the DNA has many informational gaps, there are no actual gaps in the molecule itself. The spaces between the base pairs are simply to aid in visualization.*

Microbial Sidebars replace the boxed inserts. These illustrated vignettes were designed and written to be interesting, timely and related to each chapter's central theme. ▶

NAVIGATION



1

MICROORGANISMS AND MICROBIOLOGY

Microorganisms are microscopic and independently living cells that, like humans, live in communities.

1

◀ **Section Numbers** keyed to page references provide an easy way to assign readings as well as an organized outline for students to review and take notes.

rier that separates the inside from the outside called the **cytoplasmic membrane** (Figure 2.1●). It is through the cytoplasmic membrane that nutrients and other substances needed by the cell enter, and waste materials and other cell products exit. Within a cell, and bounded by the cytoplasmic membrane, is a complex mixture of sub-

◀ **Figure Reference Locators** occur next to key figure references in the narrative. Requested by students, these red dots help them study more effectively by allowing them to quickly return to the narrative after viewing a figure.

Concept Links, signaled with a blue chain link (∞), alert students that a concept is related to material from other areas of the text. Each link refers students to a section number for quickly reviewing the related material, helping them to continually make connections between concepts. ▶

In a typical Winogradsky column a mixture of organisms develops. Algae and cyanobacteria appear quickly in the upper portions of the water column; by producing O_2 these organisms help to keep this zone oxic. Decomposition processes in the mud lead to the production of organic acids, alcohols, and H_2, suitable substrates for sulfate-reducing bacteria (∞ Sections 12.18, 13.7, 17.15, and 19.13). Sulfide from the sulfate reducers triggers development of purple and green sulfur bacteria (anoxygenic phototrophs, ∞ Sections 12.2 and 12.32) that use sulfide as a photosynthetic electron donor. These organisms typically appear in

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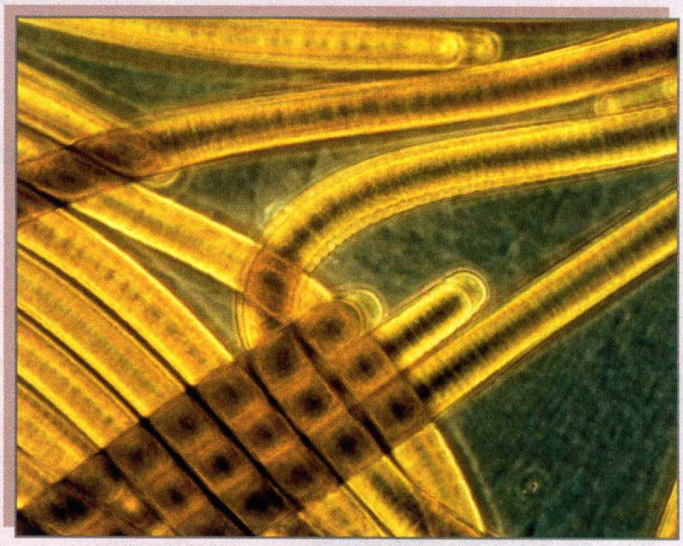
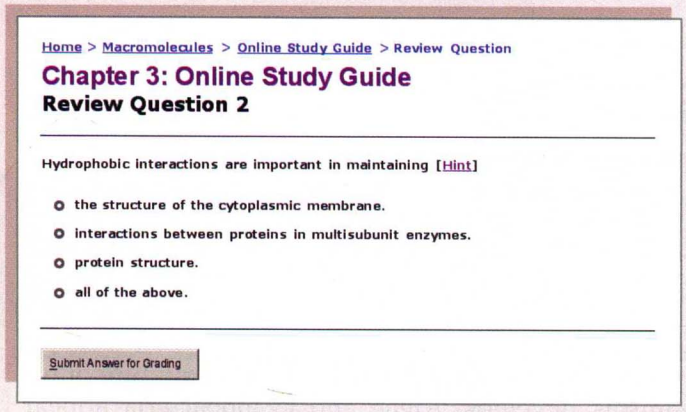


COMPANION WEBSITE



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Transcription
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Enzyme Regulation
Negative Control of Transcription and the *lac* Operon
Attenuation and the Tryptophan Operon
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The Molecular Basis for Mutations
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Generating Phylogenetic Trees from RNA Sequences
Cell Division in Conventional, Budding, and Stalked Bacteria
Bacteriorhodopsin and Light-Mediated ATP Synthesis
Life Cycle and Mating Type Switching in a Typical Yeast
DNA Chips
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Electron Transport Processes: Aerobic and Anaerobic Conditions
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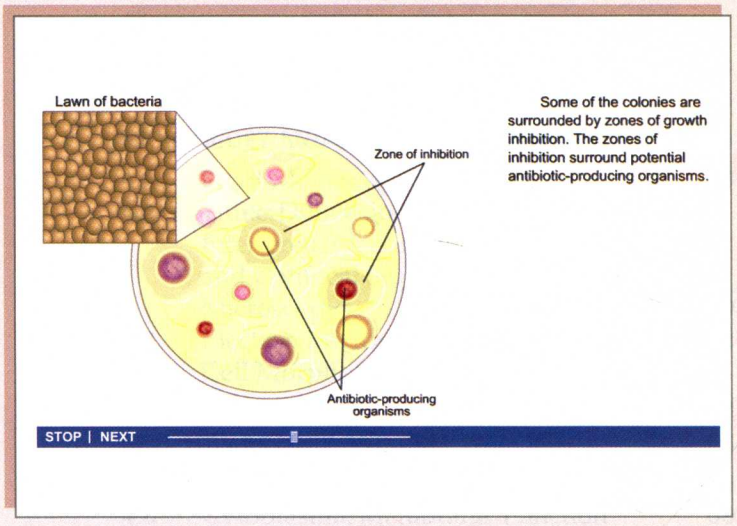
Serial Dilutions and a Most-Probable Number Analysis



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PREFACE

We are living in the age of microbiology. Almost daily come reports of new discoveries in this exciting science—new emerging infections, new organisms, and new tools to facilitate discovery. Such is the pace of the science of microbiology today. And here to bring you the up-to-the-minute picture of microbiology today is the eleventh edition of *Brock Biology of Microorganisms (BBOM)*

This textbook has roots going back over 35 years. Since the publication of the first edition of *Biology of Microorganisms* by Thomas D. Brock (Prentice Hall, 1970), this book has had a single mission: to present the principles of microbiology within the framework of modern science. *BBOM 11/e* maintains this tradition, and speaks with the same accuracy and authority of the previous ten editions.

Microbiology today places unusual demands on students and instructors alike. The amount of information is enormous, the background required in supporting sciences is significant, and introductory classes in microbiology are bursting at the seams. The authors of *BBOM 11/e* are keenly aware of these problems and have worked hard to craft a textbook of microbiology where the principles stand up and shout, the details are complementary, and the supporting concepts are well integrated. We hope you will agree.

What's New in the 11th Edition?

Those who have taught from *BBOM* in the past will find the new edition the same old friend they knew before. However, instructors will find *BBOM 11/e* more teachable, and students will find it a more invaluable learning resource, than ever before.

BBOM 11/e is pedagogically geared towards today's visual learner. The design of *BBOM 11/e* starts where the tenth edition left off, but charts new ground in terms of presentation, use of color, and art. The chapters are organized around the logical and helpful numbered outline system, present in this book from the first edition. But we have now organized each chapter into several blocks of related information, integrating the concepts into more digestible bites. As usual, a working glossary—the student's dictionary of essential terms—opens each chapter, to bring the language of microbiology where it needs to be, up front and center. Concept checks remain and are now signaled by a bright red "stop sign!" Concept checks signal the student to stop, review, and assess, before proceeding to the next concept. As usual, challenging review and application study questions are present at the end of each chapter. A comprehensive glossary and index in the back of the book, wrap up the package.

Traditional "boxed" material is presented in *BBOM 11/e* in our new *Microbial Sidebars*. These richly illustrated vignettes were designed and written to be "fun reads" of enrichment material related to a chapter's central theme. Tables have been completely redesigned in *BBOM 11/e* to make the information in them easier to follow and better organized. Since a science like microbiology relies heavily on tabular resources, the new table design should be a winner with both students and instructors alike. Many other pedagogically useful features will make themselves obvious to the reader as s/he proceeds through this book. These include more distinctive heads, an eye-catching red dot icon that leads the reader's eye from text to figures and back again, and review questions keyed to section number. The latter will make it easier for students to refresh their memories before answering each question.

Pervading the entire book is a spectacular art program, with every piece of art redone by a new art studio. The result is brighter, more distinctive art, which is also more colorful, appealing, impeccably consistent, and instructive than ever before. Moreover, the use for the first time of a high quality, glossy paper in the eleventh edition, has brought out the best in the outstanding photomicrographs and other photos that have been a tradition in this book since the first edition. Users will quickly recognize new pedagogical aids, such as our "energy arrows," built right into the art. Cellular reactions that produce or consume ATP are often key ones. Energy arrows—bright red wavy arrows—signal these reactions and bring them to a student's attention.

Although *BBOM 11/e* is actually shorter than the previous edition, it contains substantial new content. Indeed, new material can be found in every chapter and we give only a taste of what's in store here: Toxic Forms of Oxygen (Chapter 6); Diversity of Sigma Factors, Consensus Sequences, and Other RNA Polymerases (Chapter 7); The Stringent Response (Chapter 8); RNA Regulation and Riboswitches (Chapter 8); Sub-Viral Particles (Chapter 9); The Carbon and Energy Metabolism of Primitive Life Forms (Chapter 11); The Biology of *Nanoarchaeum* (Chapter 13); RNA Processing and Ribozymes (Chapter 14); Replication of Linear DNA (Chapter 14); Annotating the Genome (Chapter 15); Bioinformatic Analyses and Gene Distribution in Prokaryotes (Chapter 15); Microarrays and the Transcriptome (Chapter 15); Viruses of *Archaea* (Chapter 16); Environmental Genomics (Chapter 18); Host Risk Factors for Infection (Chapter 21); Inflammation, Fever, and Septic Shock (Chapter 22); Natural Immunity (Chapter 22); Receptors and Immunity (Chapter 23); West Nile Virus (Chapter 27); Microbial Sampling and Food Poisoning (Chapter 29); Severe Acute Respiratory Syndrome (SARS) (Chapter 25); Anthrax as a Biological Weapon (Chapter 25); and Fermented Foods (Chapter 29).

Several supplements accompany *BBOM 11/e.* These include a website (***www.prenhall.com/madigan***) con-

taining online media resources (flagged by an icon in the text), practice exam questions, and additional content resources. For instructors, a CD is available that contains *all* of the tables and figures in the book arranged in PowerPoint format for ease in organizing classroom learning activities. Overhead transparencies are also available for those who use this format in the classroom. Indeed, the *BBOM 11/e* instructor package offers every necessary tool for developing clear, compelling, and stimulating presentations.

Acknowledgments

The final product you see before you is the collective effort of many people. These include a number of folks at Prentice Hall/Pearson Publishing, but especially Executive Editor Gary Carlson and his assistants Susan Zeigler and Jennifer Hart, and our outstanding production editor, Debra Wechsler. Gary was the guiding light for this edition, while Susan/Jennifer and Debra maintained the pace of the project and were the "glue" in editorial and production, respectively. Ed Thomas (production) is also acknowledged for production assistance early in the project. The authors give a hearty thanks to the input of our design and art editors, Kenny Beck and Jay McElroy, and our superb media editors, Patrick Shriner and Crissy Dudonis. Excellent copy-editing of the entire manuscript was done by Jane Loftus (Clackamas, OR).

The authors especially wish to thank the thorough and very helpful input early on in the project of the development editor, Jon Haber (New York, NY), and the expert assistance with electronic photographs provided by Deborah O. Jung (Carbondale, IL). The excellent input of Elizabeth McPherson (University of Tennessee) and David Crowley (University of California-Riverside) as accuracy checkers during the production of *BBOM 11/e* is heartily acknowledged. Special thanks are also extended to Gernot Arp and Christian Boeker, Universität Göttingen, Germany and Carl Zeiss, Inc., Jena, Germany for the gorgeous confocal micrograph that graces the covers of this book.

Both authors also wish to thank their graduate students, colleagues, and Department of Microbiology staff for their assistance and patience during the busy time of preparing a book of this scope. The seemingly endless patience of our wives, Nancy and Judy, for the countless hours spent away from them during the development and production of *BBOM 11/e*, is also acknowledged. Their love, understanding, and support allowed the authors to devote the time necessary for such a massive project.

Finally, we are extremely grateful for the kind help of so many individuals that provided reviewer input into the draft manuscript or who supplied new photos for the 11th edition. They are listed below.

Laurie Achenbach, *Southern Illinois University*
Richard Adler, *University of Michigan-Dearborn*
Karen Aguirre, *Clarkson University*
Stephen Aley, *University of Texas-El Paso*
Mary Allen, *Hartwick College*
Ricardo Amils, *University Autonoma, Madrid, Spain*
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Biao Ding, *Ohio State University*
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Paul Dunlap, *University of Michigan*
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Elizabeth Ehrenfeld, *Southern Maine Community College*
Bruce Farnham, *Metropolitan State University-Denver*
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George Garrity, *Michigan State University*
Claire Geslin, *Université de Bretagne Occidentale, France*
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Johannes Imhoff, *Universität Kiel, Germany*
Mary Johnson, *Indiana University*
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Nancy Spear, *Murphysboro, Illinois*
Julia Thompson, *American Society for Microbiology*
Sonia Tiquia, *University of Michigan*
David Tison, *Multicare Health Systems*
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Alexander Worden, *University of Miami*
Mark Young, *Montana State University*
Stephen Zinder, *Cornell University*

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