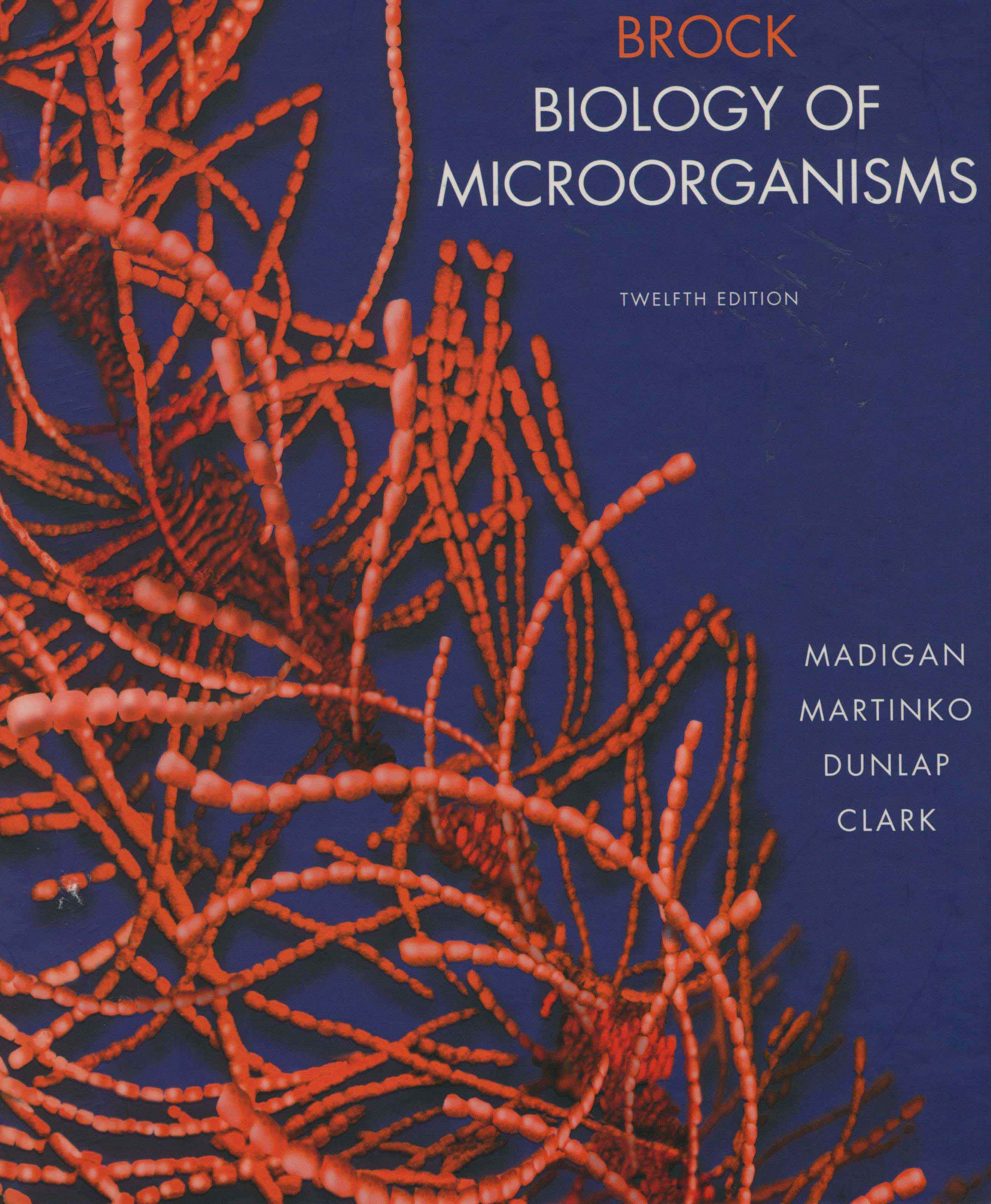

BROCK BIOLOGY OF MICROORGANISMS

TWELFTH EDITION

MADIGAN
MARTINKO
DUNLAP
CLARK

BROCK

Biology of Microorganisms

TWELFTH EDITION

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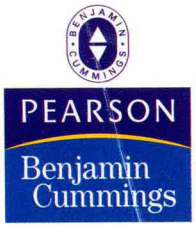

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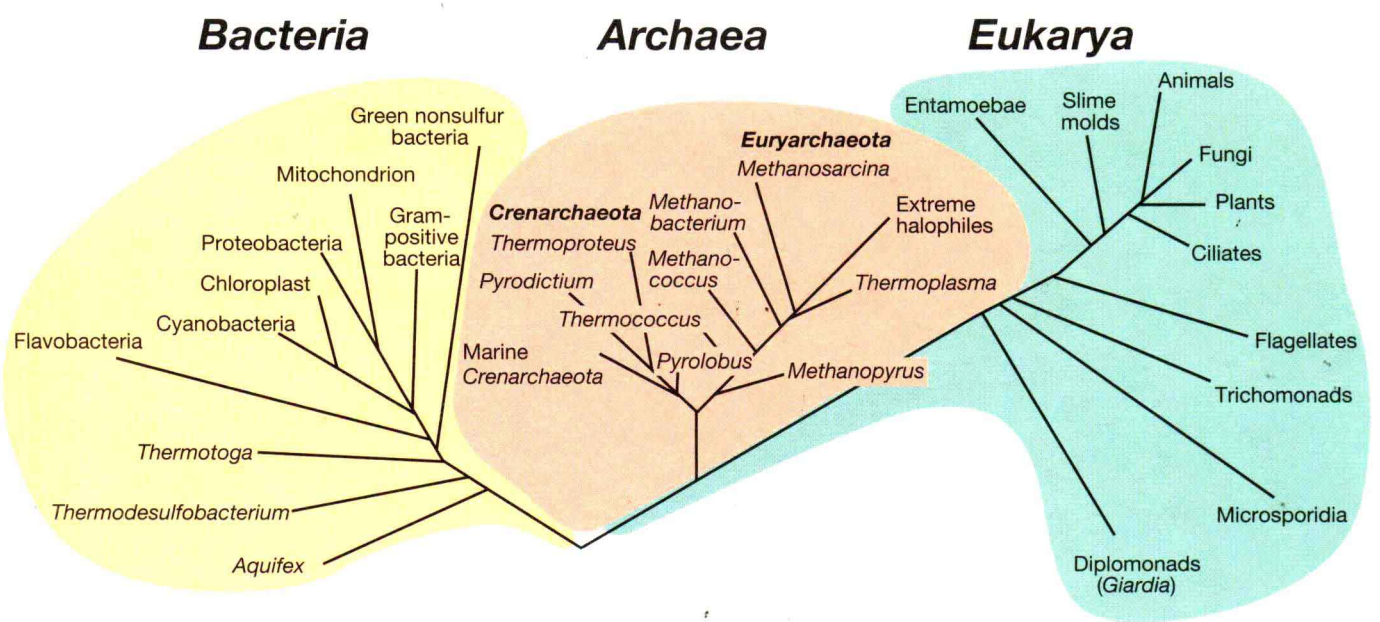
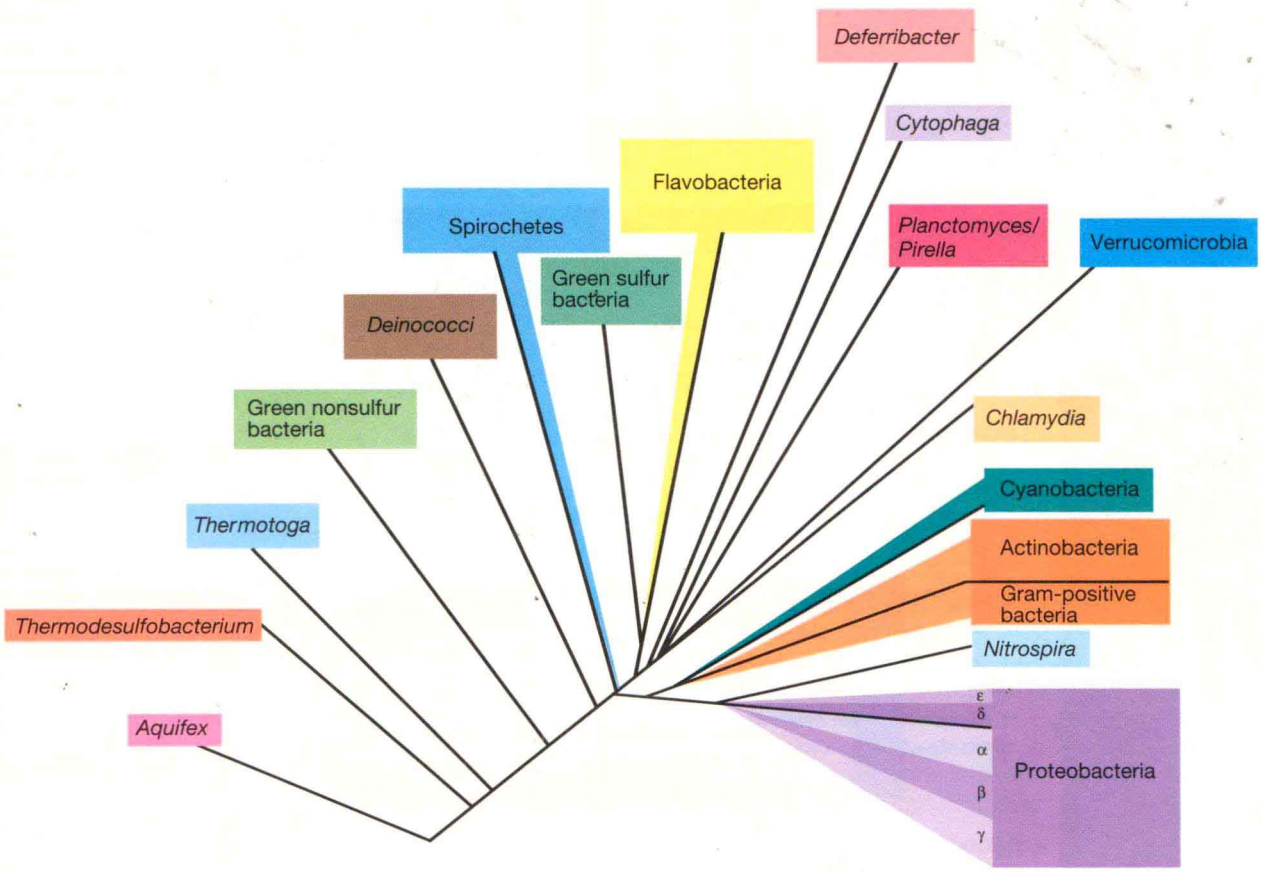
PHYLOGENY OF THE LIVING WORLD
OVERVIEW



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 14.5–14.9 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

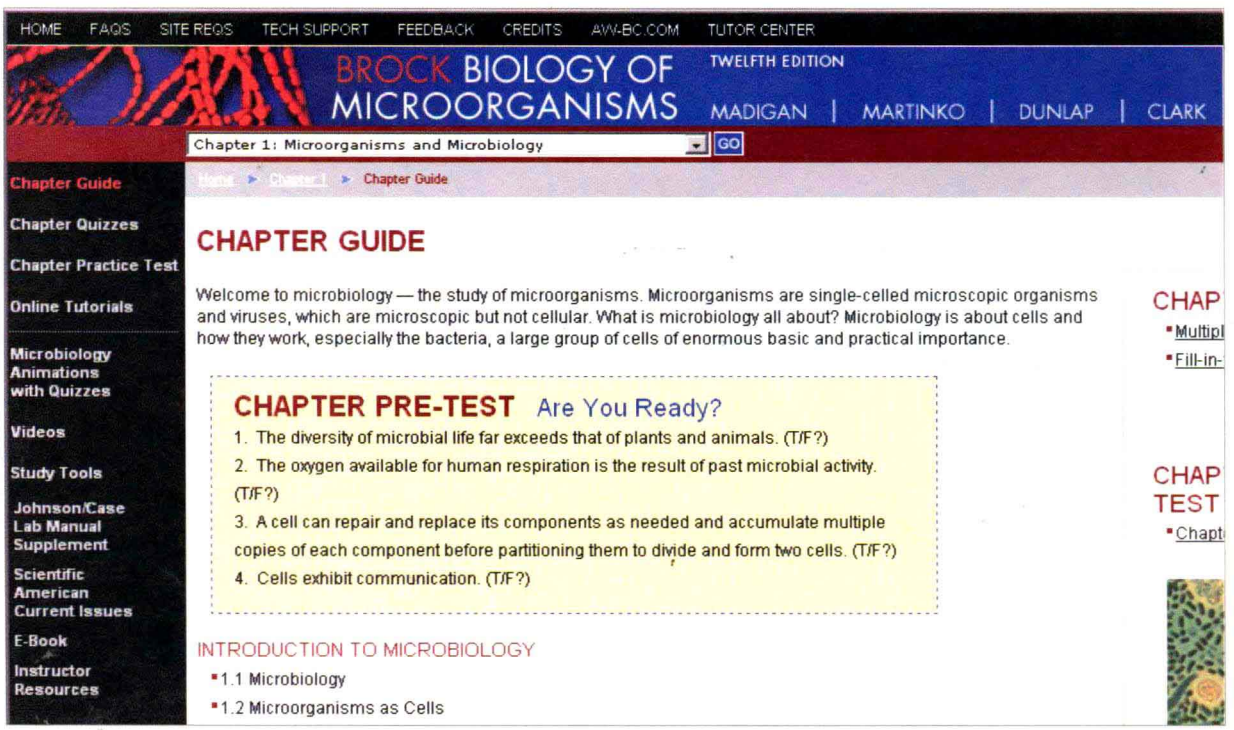


Phylogenetic Tree of *Bacteria* This tree is derived from 16S ribosomal RNA sequences. At least 17 major groups of *Bacteria* can be defined as indicated. Many other groups are known from environmental DNA but do not yet contain cultured representatives. See Sections 14.5–14.9 for further information on ribosomal RNA-based phylogenies. *Data for the tree obtained from the Ribosomal Database project* **http://rdp.cme.msu.edu**

A WEALTH OF ONLINE RESOURCES AND TOOLS

The Microbiology Place Website

This companion website for ***Brock Biology of Microorganisms*, Twelfth Edition** includes chapter guides, chapter quizzes, chapter practice tests, online tutorials, animations with quizzes, videos, study tools (interactive flashcards and a glossary), and an e-book. This greatly expanded website also includes a password-protected Instructor's Resource Section with a gradebook and other time-saving features.
www.microbiologyplace.com



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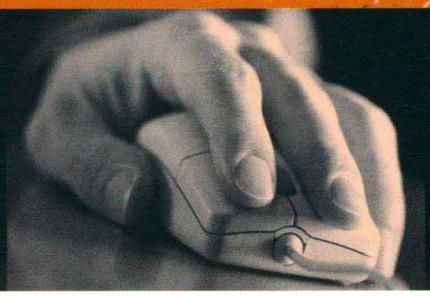
CourseCompass™ combines the strength of the content of The Microbiology Place companion website with state-of-the-art eLearning tools. CourseCompass™ is a nationally hosted, dynamic, interactive online course management system powered by Blackboard, the leading platform for web-based learning tools. This easy-to-use and customizable program enables professors to tailor content and functionality to meet individual course needs. The course includes all of the content found on The Microbiology Place website together with the complete Test Bank and also course management functionality (such as discussion boards).
www.coursecompass.com



Log on.

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5. Using a coin, scratch off the silver coating below to reveal your access code.
   Do not use a knife or other sharp object, which can damage the code.
6. Enter your access code in lowercase or uppercase, without the dashes.
7. Follow the on-screen instructions to complete registration.
   During registration, you will establish a personal login name and password to use for logging into the website. You will also be sent a registration confirmation email that contains your login name and password.

Your Access Code is:

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Instructors have the option of creating an online class for you to use with this website. If your instructor decides to do this, you'll need to complete the following steps using the Class ID your instructor provides you. By "joining a class," you enable your instructor to view the scored results of your work on the website in his or her online gradebook.

To join a class:

1. Log into the website. For instructions, see "STEP 2: Log in."
2. Click **"Join a Class"** near the top right.
3. Enter your instructor's **"Class ID"** and then click **"Next"**.
4. At the Confirm Class page you will see your instructor's name and class information. If this information is correct, click **"Next"**.
5. Click **"Enter Class Now"** from the Class Confirmation page.

- *To confirm your enrollment in the class, check for your instructor and class name at the top right of the page. You will be sent a class enrollment confirmation email.*
- *As you complete activities on the website from now through the class end date, your results will post to your instructor's gradebook, in addition to appearing in your personal view of the Results Reporter.*

To log into the class later, follow the instructions under "STEP 2: Log in."

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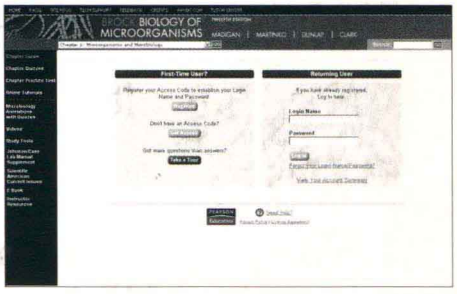
WINDOWS
OS: Windows 2000, XP
Resolution: 1024 x 768
Plugins: Latest version of Flash/QuickTime/Shockwave (as needed)
Browsers: Internet Explorer 6.0; Firefox 1.0
Internet Connection: 56k minimum

MACINTOSH
OS: 10.2.4, 10.3.2
Plugins: Latest version of Flash/QuickTime/Shockwave (as needed)
Browsers: Firefox 1.0; Safari 1.3
Internet Connection: 56k minimum

Register and log in



Join a Class

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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 centered on 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, Dr. Madigan moved to Southern Illinois University Carbondale, where he has been a professor of microbiology for nearly 30 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 he was selected as the outstanding teacher in the SIU 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 Undergraduate Teaching from the American Society for Microbiology.

Dr. Madigan's research has primarily dealt with anoxygenic phototrophic bacteria, especially species that inhabit extreme environments, and he has graduated over 20 masters and doctoral students. He has published over 110 research papers, has coedited a major treatise on phototrophic bacteria, and has served as chief editor of the journal *Archives of Microbiology*. He currently serves on the editorial board of the journal *Environmental Microbiology*.

Mike's nonscientific interests include tree planting and caring for his dogs and horses. He lives beside a quiet lake about five miles from the SIUC campus with his wife, Nancy, four shelter dogs (Gaino, Snuffy, Pepto, and Merry), and three horses (Springer, Feivel, and Festus).

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 worked for two years at Case Western Reserve University, 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 director of the Molecular Biology, Microbiology, and Biochemistry Graduate Program.

Dr. Martinko's current research involves manipulating immune reactions by inducing structural mutations in single-chain peptide–major histocompatibility protein complexes. He teaches undergraduate and graduate courses in immunology, and he also teaches immunology, host defense, and infectious disease topics in a general microbiology course as well as to medical students.

John has been active in educational outreach programs for pre-university students and teachers. For his educational efforts, he won the 2007 Southern Illinois University Outstanding Teaching Award. He is also an avid golfer and cyclist. John lives in Carbondale with his wife, Judy, a high school science teacher.

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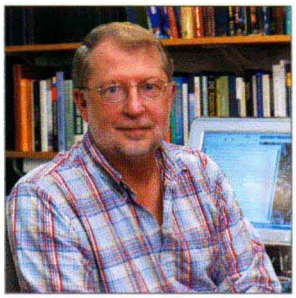
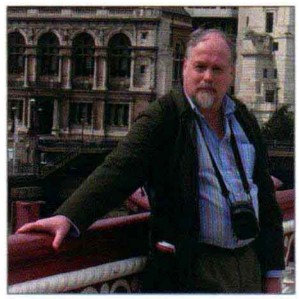


Paul V. Dunlap received his B.S. degree in microbiology from Oregon State University in 1975. As an undergraduate student, he participated in research in marine microbiology in the laboratory of R.Y. Morita and served in his senior year as a teaching assistant for courses in microbiology, gaining experience in laboratory and field research and in teaching. He then taught English in Japan until 1978, when he returned to the United States for graduate studies in biology with J.G. Morin at UCLA. Research for his Ph.D. degree, awarded in 1984, addressed the ecology and physiology of bioluminescent symbiosis. He then moved to Cornell University in Ithaca, New York, for postdoctoral studies with E.P. Greenberg on the genetic regulation of bacterial luminescence.

In 1986 Dr. Dunlap joined the faculty at New Mexico State University and in 1989 moved to the Biology Department at the Woods Hole Oceanographic Institution, where he worked for several years on quorum sensing and symbiosis in luminous bacteria before moving in 1996 to the University of Maryland's Center of Marine Biotechnology in Baltimore. In 2001, he joined the faculty of the University of Michigan in Ann Arbor, where he is an associate professor in the Department of Ecology and Evolutionary Biology.

Dr. Dunlap's research focuses on the systematics of luminous bacteria, microbial evolution, bioluminescent symbiosis, and quorum sensing. He teaches an undergraduate majors course in introductory microbiology and a senior/graduate level course in microbial diversity.

Paul's nonscientific interests include family history research and the practice of aikido, a Japanese martial art. He lives in Ann Arbor with his wife, daughter, and their Australian terrier.



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 to become a postdoctoral researcher 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. He joined the faculty of Southern Illinois University Carbondale in 1981.

Dr. Clark's research has focused on the growth of bacteria by fermentation under anaerobic conditions. He has published over 70 research articles and graduated over 20 masters and doctoral students. In 1989 he won the 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. He is the author of two books: *Molecular Biology, Made Simple and Fun*, now in its third edition, and *Molecular Biology, Understanding the Genetic Revolution*.

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 his wife Nancy—the apple of his eye and the love of his life.

John M. Martinko dedicates this book to his wife, Judy. Even the tough stuff is easy with you to share the load!

Paul V. Dunlap dedicates this book to R.Y. Morita with gratitude and appreciation for his mentoring and guidance in marine microbiological research.

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 are proud to present the 12th edition of *Brock Biology of Microorganisms* (*BBOM 12/e*). The roots of this book go back nearly 40 years, but its main objective has never wavered: to present the basic principles of microbiology in a clear and exciting way. We hope that the 12th edition of what is now a textbook classic continues in this vein and inspires a new generation of microbiologists to choose careers in this fascinating field.

Microbiology today places unusual demands on students and instructors alike. It also places unusual demands on textbook authors. The knowledge base in microbiology is simply enormous, and as authors, our job is to describe the principles along with a reasonable amount of supporting material. Thus, to maintain the authority that users of this book have become accustomed to, and also to keep the book within bounds, two new coauthors have joined the *BBOM* author team. David Clark, an expert in bacterial genetics and molecular biology and the author of two popular textbooks in molecular biology, has authored the chapters in *BBOM* that deal with these topics. Paul Dunlap, an expert in bacterial systematics and microbial evolution, has authored the microbial diversity and evolution chapters. Madigan and Martinko have authored the remaining chapters. Along with our publisher, Benjamin Cummings, who took over this project midstream from Prentice Hall, we feel we have produced a book that both students and instructors will find enticing and exciting.

WHAT'S NEW IN THE 12TH EDITION?

Instructors who have taught from *BBOM* in the past will be quite comfortable with this new edition. As usual, the chapters are organized into modules by numbered head, which allows instructors to build their courses as they see fit. In addition, study aids and review tools are an integral part of the text. Our new MiniReviews feature, which debuts with the 12th edition, is intended to refresh students' understanding and challenge their mastery of the principles as they work their way through a chapter. Also new to this edition is the location of the newly-named Review of Key Terms feature, which now summarizes a chapter's key terms and complements the challenging review questions that form the heart of the end-of-chapter review materials. A comprehensive glossary and index wrap up the learning package.

All of these learning aids are displayed in a new, more open design that gives the figures and other elements in the book some breathing room and has allowed us to present the material in a more visually appealing way. Supporting the narrative is a spectacular illustration program, with every piece of art revised as needed for content, clarity, or color contrast. The distinctive illustrations are accurate and highly instructive. The art complements (and in many cases integrates) the hundreds of photos in this text, many of which are new to this edition.

Our Microbial Sidebars in *BBOM 12/e* are fun reads of enrichment material related to chapter themes. Several new Microbial Sidebars were written for this edition, including "Microbial Growth in the Real World: Biofilms" (Chapter 6); "Did Viruses Invent DNA?" (Chapter 10); "Mimivirus and Virus Evolution" (Chapter 19); "Synthetic Biology and Bacterial Photography" (Chapter 26); "Probiotics" (Chapter 28); "SARS as an Example of Epidemiological Success" (Chapter 33); "Special Pathogens and Viral Hemorrhagic Fevers" (Chapter 35); and "Spinach and *Escherichia coli* O157:H7" (Chapter 37).

Although the 12th edition is about the same length as the 11th edition, careful editing by the author team has allowed several new chapters to debut in this edition. Chapter 8 (Archaeal and Eukaryotic Molecular Biology) focuses on the molecular biology of *Archaea* and their relationships to eukaryotic cells. Chapter 12 (Genetic Engineering) describes the tools that underlie the revolution in molecular biology. Chapter 14 (Microbial Evolution and Systematics) is a fresh new approach to issues surrounding the origin of life and microbial evolution. Chapter 26 (Biotechnology) reviews the basic science behind the biotech revolution and presents several spectacular examples of the benefits of biotechnology to human medicine, and plant and animal agriculture. Chapter 30 (Immunology in Host Defense and Disease) pulls together many of the applied aspects of immunology and shows how the immune response keeps us healthy. Coupled with these new chapters are many heavily reworked chapters. Readers will especially appreciate the more phylogenetic approach to the systematics of both prokaryotes and eukaryotes in this new edition as well as the expanded ecology material that includes some exciting and experimentally tractable microbial symbioses. Material on microbial genomics has also been greatly updated to reflect the pace and excitement of research in this area today.

CHAPTER-BY-CHAPTER REVISIONS

BBOM 12/e is *the* textbook of microbiology for both the beginning student and the seasoned researcher; it displays the perfect mix of principles and details. Major topics include general principles (structure/function, metabolism and growth), molecular biology/genetics, genomics, evolution and microbial diversity, metabolic diversity, microbial ecology, biotechnology and industrial microbiology, control of microbial growth, basic and applied immunology, and complete coverage of infectious diseases organized by mode of transmission. In addition, *BBOM 12/e* maintains a theme of evolution and ecology from beginning to end and is the only book that recognizes the importance and unique biology of *Archaea*. See highlights as follows.

Chapter 1

- New coverage on the antiquity and extent of microbial life and on careers in microbiology
- Expanded coverage of the contributions of Louis Pasteur

Chapter 2

- Broad coverage of all forms of microscopy
- An updated snapshot of microbial diversity

Chapter 3

- The essentials of cell chemistry with an emphasis on what students really need to know to understand how cells work

Chapter 4

- A streamlined chapter focused on the principles of prokaryotic cell structure and function

Chapter 5

- New discussion on the chemical elements of life
- Major coverage of catabolic principles plus an overview of essential anabolic reactions
- A new box entitled "The Products of Fermentation and the Pasteur Effect" that ties together the concepts of fermentation and respiration

Chapter 6

- Expanded coverage of cell division processes supported by spectacular new art and color photos
- A new box entitled "Microbial Growth in the Real World: Biofilms"

Chapter 7

- A substantially revised treatment that brings together the essential principles of molecular biology in *Escherichia coli*, the model species of *Bacteria*

Chapter 8

- A brand-new chapter that compares/contrasts the molecular biology of *Archaea* with that of *Eukarya* and *Bacteria*
- A new box entitled "Inteins and Protein Splicing"
- Coverage of RNA interference (RNAi), research that garnered a 2006 Nobel Prize

Chapter 9

- Major updates of the regulation of gene expression, one of the hottest areas in microbiology today
- New material on negative and positive control, global control, quorum sensing, gene regulation in *Archaea*, regulation of sporulation in *Bacillus*, the *Caulobacter* life cycle, and RNA-based regulation

Chapter 10

- The essential principles of virology plus a snapshot of viral diversity
- New coverage of subviral entities, including prions and viroids
- An intriguing new box entitled "Did Viruses Invent DNA?"

Chapter 11

- A streamlined chapter that now deals exclusively with bacterial genetics: chromosomes and plasmids, mutation, and genetic exchange
- New coverage of genetic exchange in *Archaea*

Chapter 12

- A discussion of modern *in vitro* molecular methods, molecular cloning, and genetic manipulations, all brought together in one chapter as a prelude to genomics

Chapter 13

- Microbial genomics as we know it today. Coverage of genome function and regulation, the evolution of genomes, and the exciting field of metagenomics

Chapter 14

- New detailed coverage of the origin of life and endosymbiosis
- Expanded coverage of theoretical and analytical aspects of molecular evolution and microbial phylogeny

Chapters 15–17

- Prokaryotic diversity presented in a phylogenetic context. Chapter 15 covers all five subdivisions of *Proteobacteria*, and Chapter 16 covers other well-studied lineages of *Bacteria*. Chapter 17 updates the biology of *Archaea*.
- Spectacular photo- and electron micrographs that guide the reader through the diversity of *Bacteria* and *Archaea*
- All bacterial names updated to the latest in nomenclatural standards

Chapter 18

- A revised treatment of the cell biology and diversity of microbial eukaryotes
- A truly phylogenetic rather than taxonomic treatment of eukaryotic microbial diversity based on multiple gene and protein analyses

Chapter 19

- Viral diversity from bacteriophages through animal and plant viruses organized by replication mechanism
- An exciting new box focused on giant viruses entitled "Mimivirus and Virus Evolution"

Chapters 20–21

- Coverage of metabolic diversity in two reorganized chapters that group related processes: Chapter 20, phototrophy, chemolithotrophy, and important biosyntheses; Chapter 21, catabolism of organic compounds
- Coverage of new metabolic processes, such as proton reduction as an anaerobic respiration and the mechanism of anoxic hydrocarbon oxidation

Chapter 22

- All the latest methods in microbial ecology, including new coverage of cutting-edge methods such as phylochips, T-RFLP, and stable isotope probing

Chapter 23

- Principles of microbial ecology and descriptions of major microbial habitats
- Expanded coverage of biofilms, including new photos of the development of *Pseudomonas aeruginosa* biofilms

Chapter 24

- Microbial ecology with a focus on nutrient cycles, bioremediation, and microbial animal and plant symbioses
- New, richly illustrated coverage of the *Aliivibrio*–squid symbiosis

Chapter 25

- The principles behind major commercial microbial fermentations
- Expanded coverage of wine production

Chapter 26

- Biotechnology with the emphasis on products rather than methods
- Expanded coverage of transgenic plants and animals
- A fascinating new box entitled "Synthetic Biology and Bacterial Photography" that ties basic research into a unique microbial application

Chapter 27

- An introduction to microbial growth control, in particular, antibiotics and their mode of action
- Expanded coverage of antibiotic resistance and infection control

Chapter 28

- Revised treatment of the human normal flora based on molecular microbial community analyses
- Expanded discussion of virulence factors using *Salmonella* as an example and microbial toxins and toxin mechanisms
- A new box entitled "Probiotics" that answers the question: Do live bacterial supplements really have any benefit?

Chapters 29–31

- The world of immunology: Chapter 29 (the essentials), Chapter 30 (host defenses and applications), and Chapter 31 (immune mechanisms at the molecular level). All chapters are modular so that instructors can pick and choose topics that work best in their courses.
- Major revisions to art in all of these chapters in order to greatly improve consistency

Chapter 32

- A streamlined treatment of modern immunological and molecular methods used in clinical diagnostics

Chapter 33

- Updates of the HIV–AIDS pandemic and other important emerging infectious diseases
- A snapshot of the rapidly changing picture in healthcare-associated disease and infection control
- A new box entitled "SARS as an Example of Epidemiological Success" that connects SARS surveillance with the control of other rapidly emerging diseases

Chapter 34

- Major human diseases organized by mode of transmission
- Updated and expanded coverage of streptococcal and staphylococcal diseases and increased antibiotic resistance
- Expanded coverage of influenza and scenarios for a pandemic
- A new section on human papillomavirus infection as a preventable and treatable sexually transmitted disease that can lead to cancer

Chapter 35

- An updated chronicle of the spread of West Nile virus across the United States and the implications of this avian disease for human health
- An exciting new box entitled "Special Pathogens and Viral Hemorrhagic Fevers" that describes an important branch of the U.S. Centers for Disease Control (CDC) that deals with extremely dangerous pathogens

Chapter 36

- Expanded coverage of water quality assessment methods, including current U.S. Environmental Protection Agency standards

Chapter 37

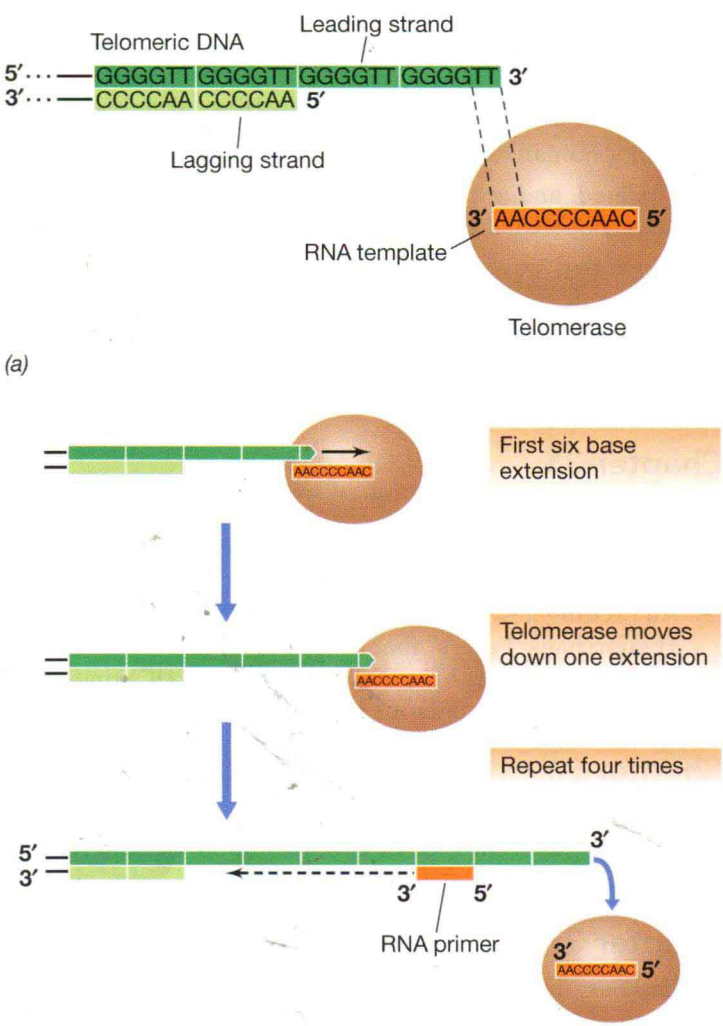
- Discussion of "aseptic processing," a new preservation method in the food industry
- An update on *Salmonella* as a food pathogen
- A timely new box entitled "Spinach and *Escherichia coli* O157:H7" that explores the transmission of this food pathogen by plant as well as animal food products

Three New Chapters on Rapidly Developing Fields

Three new chapters focus on the rapidly developing fields of archaeal and eukaryotic molecular biology, biotechnology, and immunology in host defense and disease.

CHAPTER 8: ARCHAEAL AND EUKARYOTIC MOLECULAR BIOLOGY

Molecular biology has revealed the three domains of life (*Bacteria*, *Archaea*, and *Eukarya*) and given us an unprecedented snapshot of microbial evolution. From a molecular perspective, cells of *Archaea* and *Eukarya* share much in common. The all-new Chapter 8 is the first of its kind in a microbiology textbook and compares and contrasts the molecular biology of these two domains with that of *Bacteria* (Chapter 7). Together, Chapter 7 and the new Chapter 8 give students the molecular background they need to understand microbiology today and to appreciate the science behind photos such as the one here of telomeres on eukaryotic chromosomes.



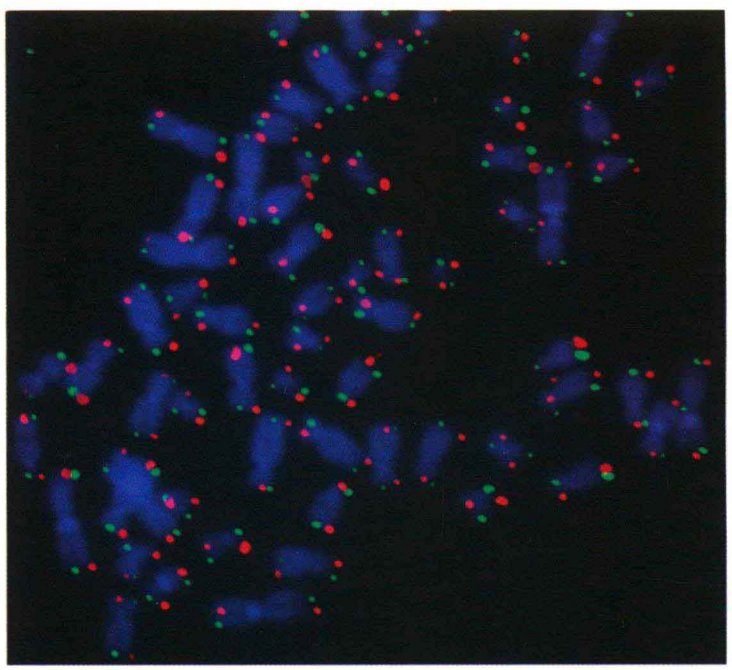


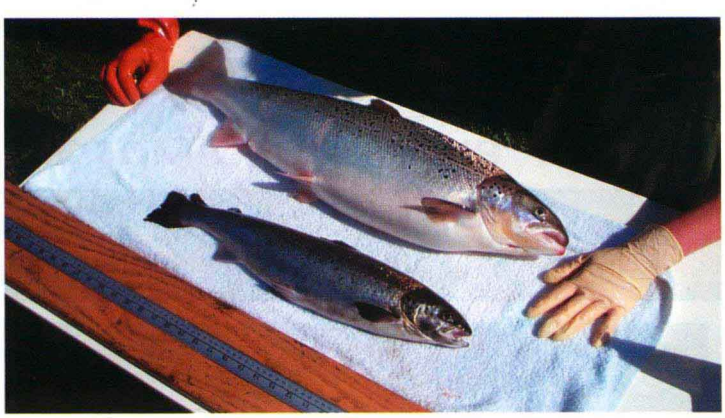
Figure 8.9 Model for the activity of telomerase at one end of a eukaryotic chromosome. *(a)* A diagram of the sequence of the end of the DNA in a telomere, with four of the guanine-rich repeats and the enzyme telomerase, which contains a short RNA template. *(b)* Steps in elongation of the guanine-rich strand catalyzed by telomerase. After telomerase finishes, the lagging strand can be primed with an RNA primer by primase followed by completion of the lagging strand by DNA polymerase and ligase. *(c)* A preparation of HeLa cell chromosomes stained with fluorescent dyes. The red dots are leading strand telomeres and the green dots are lagging strand telomeres.

CHAPTER 26: BIOTECHNOLOGY

The new Chapter 26 examines the advances in biotechnology that have generated a host of new tools for molecular biology and genomics as well as several important products for human health. Biotechnology is yielding new perspectives on genes and gene expression (see the fluorescent pig) and is playing a greater role in the food we eat (see the transgenic salmon).

Shinn-Chih Wu

(a)



Aqua Bounty Technologies

(b)

Figure 26.8 **Transgenic animals.** *(a)* A piglet (left) that has been genetically engineered to express the green fluorescent protein and thus fluoresces green under blue light. Control piglets are shown in the center and right. *(b)* Fast-growing salmon. The *AquAdvantage*™ Salmon" (top) was engineered by Aqua Bounty Technologies (St. Johns, Newfoundland, Canada). Both the transgenic and the control fish are 18 months old and weigh 4.5 kg and 1.2 kg, respectively.

CHAPTER 30: IMMUNOLOGY IN HOST DEFENSE AND DISEASE

Immunology is a major sub-discipline of microbiology, but many instructors struggle to present the key concepts. The new Chapter 30 is designed as an overview of immunology with a focus on the applied aspects that all students need to know: different forms of the immune response, principles of immunization, and autoimmunity. Instructors will find Chapter 30 to be the "one-stop shop" they need to teach immunology.

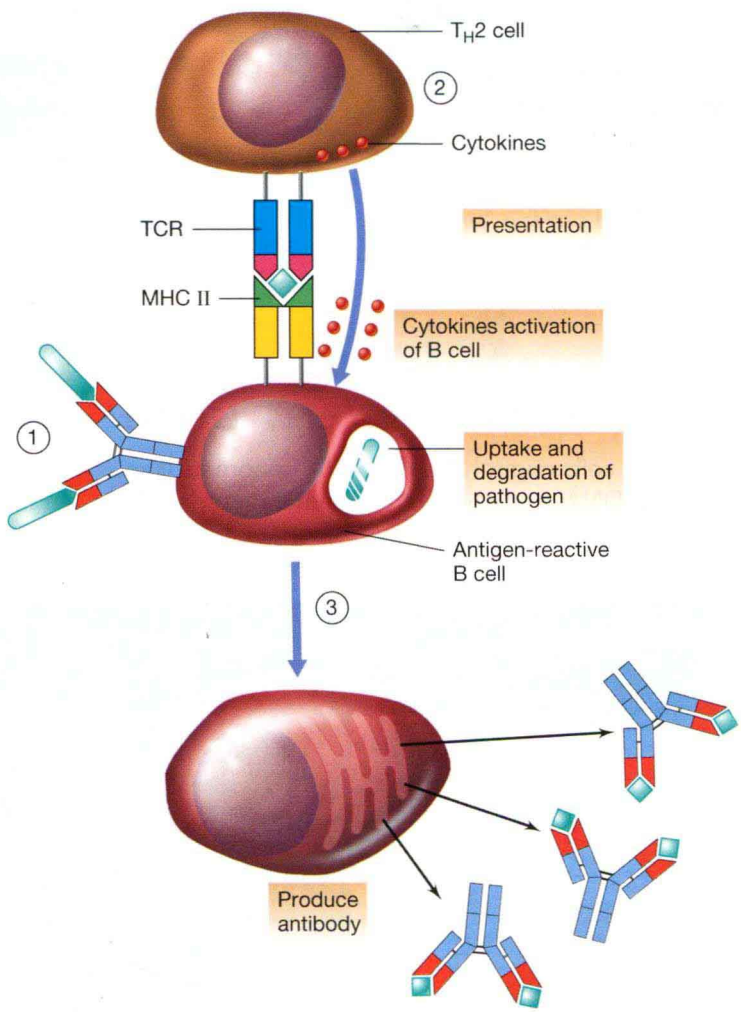


Figure 30.3 **Antibody-mediated immunity.** ① Antibody on B cells binds to a pathogen. The B cell ingests, degrades, and processes the pathogen. ② The B cell presents pathogen antigen to a T_{H2} cell, activating it to produce cytokines that in turn influence the B cell to develop into a plasma cell. ③ The plasma cell produces antibodies.

Hot Topics Integrated Throughout the Chapters

Hot topics draw students in to the chapters and introduce them to current issues in microbiology. The number of hot topics has been increased in this edition.

Microbial Sidebars present enrichment material related to a chapter's central theme.

BIOFILMS

Biofilms develop when bacterial cells attach and grow on surfaces. They are associated with some human diseases, such as cystic fibrosis. Exciting new coverage of biofilms is included in Chapters 6 and 23 and is illustrated with several spectacular photos.

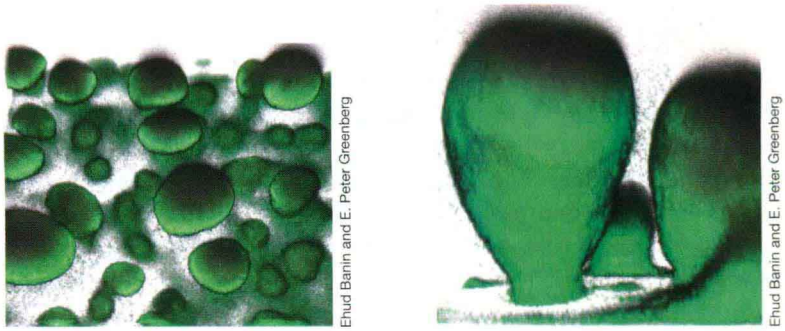
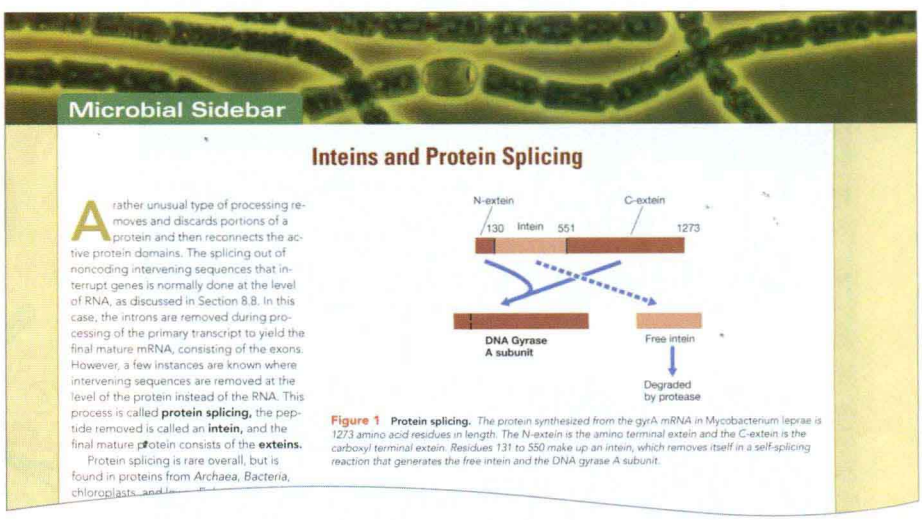


Figure 23.7 Biofilms of *Pseudomonas aeruginosa*.

INTEINS AND PROTEIN SPLICING

Self-splicing RNAs (ribozymes) have a counterpart in self-splicing proteins (inteins), found in all domains of life. Find out the "what, why, and how" of inteins in an exciting new Microbial Sidebar in Chapter 8.



Microbial Sidebar

Inteins and Protein Splicing

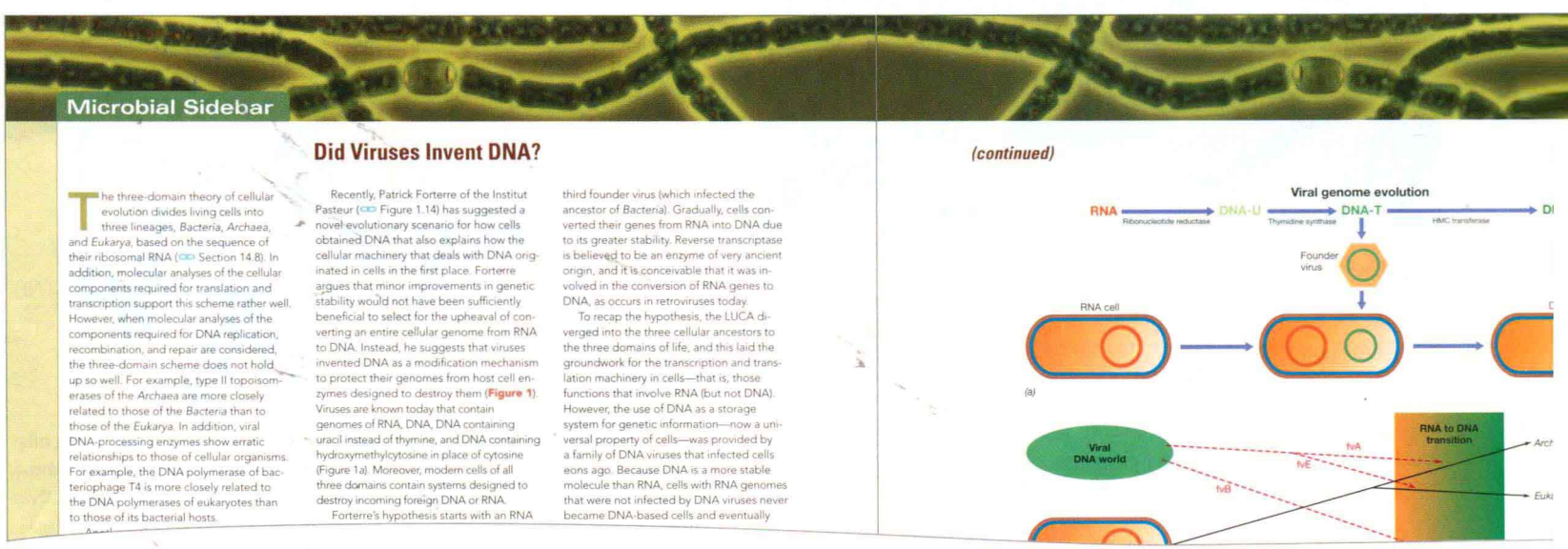
A rather unusual type of processing removes and discards portions of a protein and then reconnects the active protein domains. The splicing out of noncoding intervening sequences that interrupt genes is normally done at the level of RNA, as discussed in Section 8.8. In this case, the introns are removed during processing of the primary transcript to yield the final mature mRNA, consisting of the exons. However, a few instances are known where intervening sequences are removed at the level of the protein instead of the RNA. This process is called **protein splicing,** the peptide removed is called an **intein,** and the final mature protein consists of the **exteins.**

Protein splicing is rare overall, but is found in proteins from *Archaea, Bacteria,* chloroplasts, and

Figure 1 **Protein splicing.** *The protein synthesized from the gyrA mRNA in Mycobacterium leprae is 1273 amino acid residues in length. The N-extein is the amino terminal extein and the C-extein is the carboxyl terminal extein. Residues 131 to 550 make up an intein, which removes itself in a self-splicing reaction that generates the free intein and the DNA gyrase A subunit.*

DID VIRUSES INVENT DNA?

Primitive cells might have had RNA genomes. If so, how did DNA come to be the genetic material of all cells today? Discover the virus connection in this intriguing new Microbial Sidebar in Chapter 10.



Microbial Sidebar

Did Viruses Invent DNA?

The three-domain theory of cellular evolution divides living cells into three lineages, *Bacteria, Archaea,* and *Eukarya,* based on the sequence of their ribosomal RNA (Section 14.8). In addition, molecular analyses of the cellular components required for translation and transcription support this scheme rather well. However, when molecular analyses of the components required for DNA replication, recombination, and repair are considered, the three-domain scheme does not hold up so well. For example, type II topoisomerases of the *Archaea* are more closely related to those of the *Bacteria* than to those of the *Eukarya.* In addition, viral DNA-processing enzymes show erratic relationships to those of cellular organisms. For example, the DNA polymerase of bacteriophage T4 is more closely related to the DNA polymerases of eukaryotes than to those of its bacterial hosts.

Recently, Patrick Forterre of the Institut Pasteur (Figure 1.14) has suggested a novel evolutionary scenario for how cells obtained DNA that also explains how the cellular machinery that deals with DNA originated in cells in the first place. Forterre argues that minor improvements in genetic stability would not have been sufficiently beneficial to select for the upheaval of converting an entire cellular genome from RNA to DNA. Instead, he suggests that viruses invented DNA as a modification mechanism to protect their genomes from host cell enzymes designed to destroy them (**Figure 1**). Viruses are known today that contain genomes of RNA, DNA, DNA containing uracil instead of thymine, and DNA containing hydroxymethylcytosine in place of cytosine (Figure 1a). Moreover, modern cells of all three domains contain systems designed to destroy incoming foreign DNA or RNA.

Forterre's hypothesis starts with an RNA third founder virus (which infected the ancestor of *Bacteria*). Gradually, cells converted their genes from RNA into DNA due to its greater stability. Reverse transcriptase is believed to be an enzyme of very ancient origin, and it is conceivable that it was involved in the conversion of RNA genes to DNA, as occurs in retroviruses today.

To recap the hypothesis, the LUCA diverged into the three cellular ancestors to the three domains of life, and this laid the groundwork for the transcription and translation machinery in cells—that is, those functions that involve RNA (but not DNA). However, the use of DNA as a storage system for genetic information—now a universal property of cells—was provided by a family of DNA viruses that infected cells eons ago. Because DNA is a more stable molecule than RNA, cells with RNA genomes that were not infected by DNA viruses never became DNA-based cells and eventually

(continued)

Exceptionally Clear Illustrations and Photos

Unparalleled illustration and photo program gives students a clear and fascinating view into the microbial world.

ILLUSTRATIONS

The cytoplasmic membrane with its dense array of proteins comes alive with spectacular art.

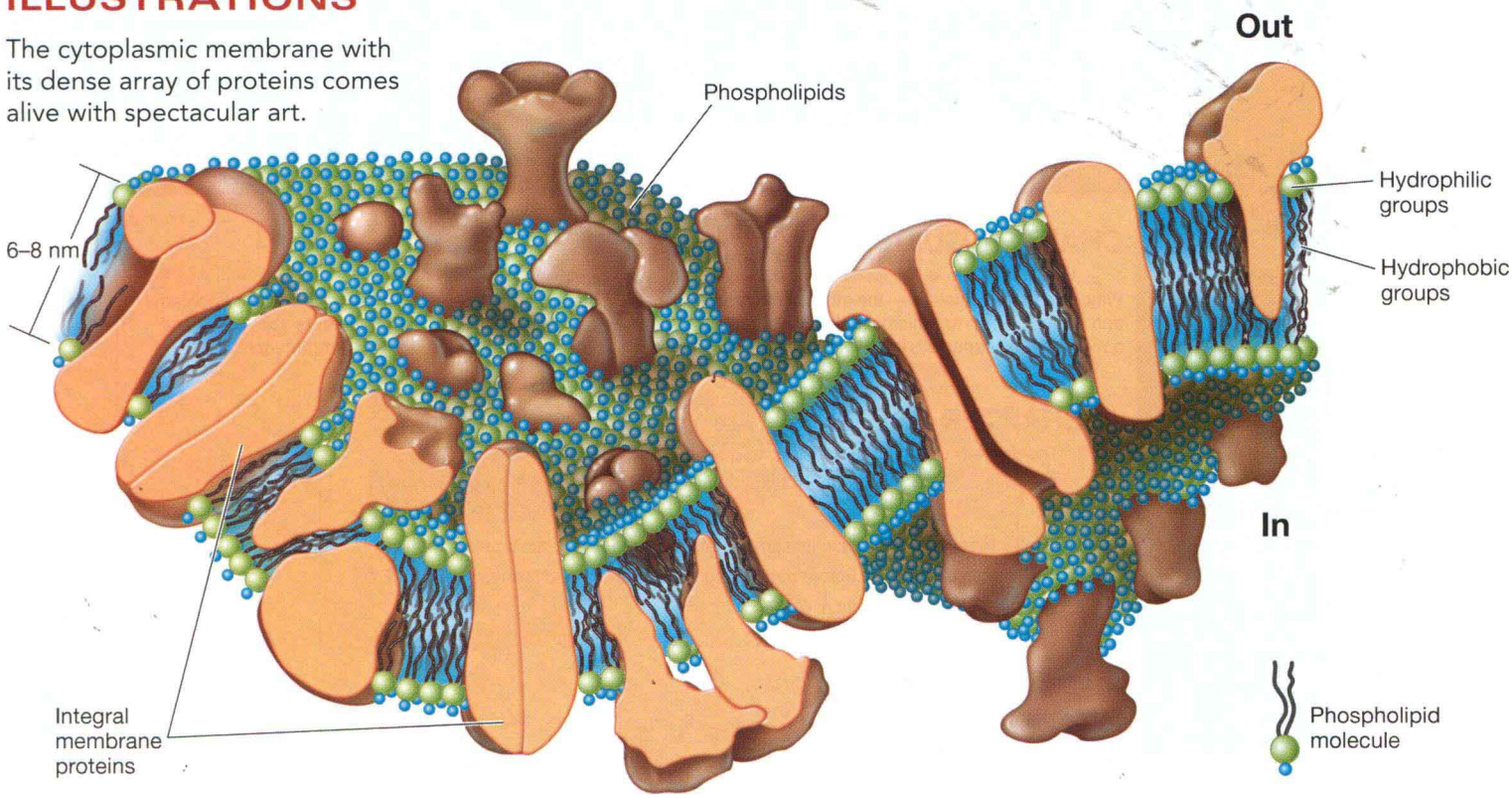
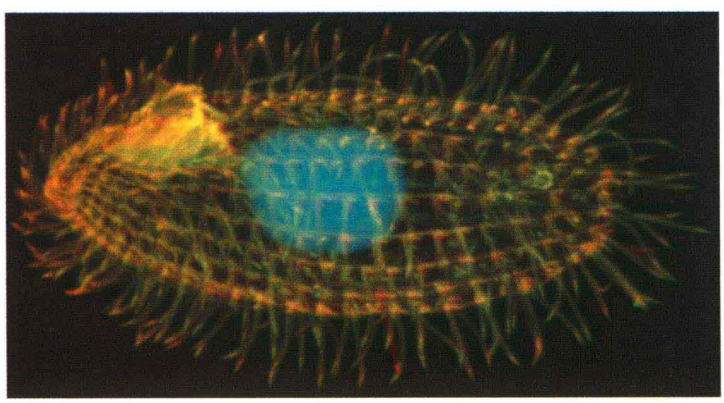


Figure 4.5 Structure of the cytoplasmic membrane.

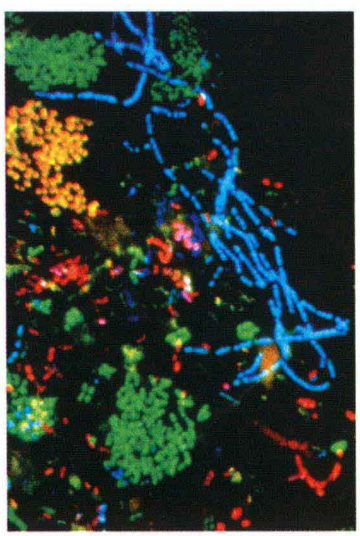
PHOTOMICROGRAPHS

The best photomicrographs of any microbiology textbook are exemplified here by a cell of the protist *Tetrahymena* stained to reveal special cellular structures.



Rupal Thazhath and Jacek Gaertig

Figure 18.10 Tubulin of *Tetrahymena thermophila*.



Michael Wagner and Jiri Snaidr

Phylogenetic stains, used here on a sewage sample, give microbial ecologists the power to both quantify microorganisms in natural samples and identify them phylogenetically.

Figure 22.11 FISH analysis of sewage sludge.

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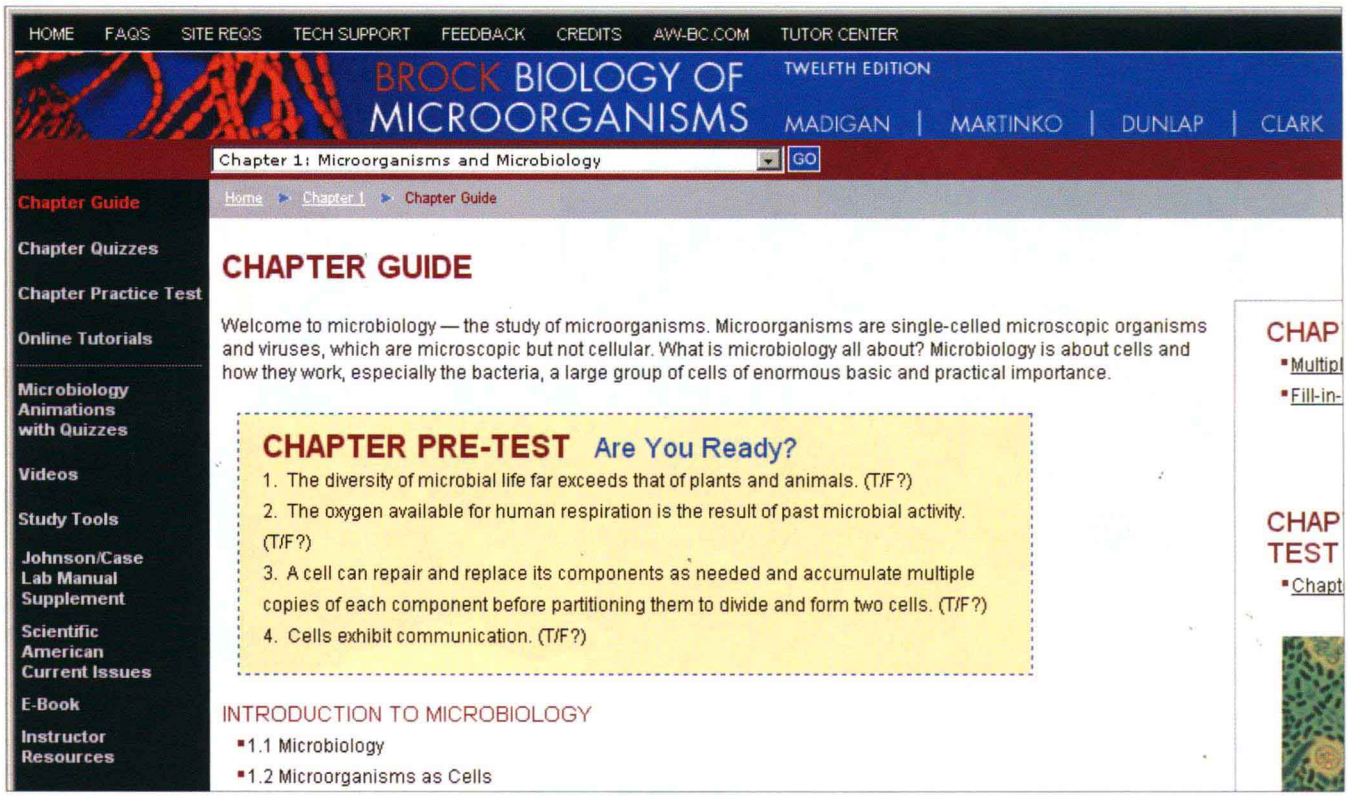

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